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THE COURSE OF EVOLUTION

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THE COURSE OF EVOLUTION

BY DIFFERENTIATION OR
DIVERGENT MUTATION RATHER THAN
BY SELECTION

by

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PREFACE

AN accident in 1905, and the nature of my official occupation, forced me to work that could be done in spare time with the aid of a pen and a library, and since then I have largely devoted myself to the study of geographical distribution. The dictionary for which I was responsible emphasised in my mind the enormous variety in sizes and distribution of families, genera, and species. All seemed a nearly hopeless confusion. Yet this is not nature's way; her work is always beautifully planned, as Darwin had already shown in the wonderful theory of evolution, whose establishment as a working guide through the intricacies of life was due to him, and gave him his lasting claim to fame. Without a mechanism to operate it, however, few were prepared to make so great a break with what had gone before. In natural selection, Darwin produced an apparently serviceable mechanism, which was so familiar to every one that it had a great appeal, soon resulting in the establishment of evolution in an unassailable position. But during the last fifty years there has always been an underlying feeling that all was not well with natural selection. The writer, though brought up in its strictest school, soon began to feel very doubtful about it, and a few years of experience with tropical vegetation made him realise that selection could not be responsible for evolution. From that time onwards he has never ceased to bring up objections to it, though rarely has any answer to these been attempted. Selection is now no longer required as a support for evolution, and must take its proper place, which is one of great importance, as has been pointed out here and elsewhere.

The writer then set out, some thirty-five years ago, to find some definite laws underlying the welter of facts in distribution. The first thing that really set him upon the track was the discovery in 1912 of the "hollow curve" formed by the numbers of species in the genera of the Ceylon flora, a curve which soon proved to be universal in both floras and faunas. This led to the development of the theory set out in *Age and Area* in 1922. Being, among other things, a flat contradiction of the theory of gradual adaptation through the agency of natural selection, this theory of age and area was not accepted, but as the counter

PREFACE

arguments brought up mostly assumed that the older theory was sound, the writer's faith remained unchanged, and he continued to follow up his beliefs. They are now yielding interesting results, of which the present book is one, while another, dealing with distribution, and which is perhaps even more subversive of current opinions (used as a shelter for so much in national policies), is upon the road to completion.

The present book, the logical sequence of *Age and Area*, has been greatly delayed by various inconveniences, and by the great quantity of statistical work required. This was so great a burden that I can hardly sufficiently express my gratitude to my friend Mr John Murray, late of the Indian Educational Department, who undertook a great deal of it, and with his trained mathematical skill was able to do it well and rapidly. I am also deeply indebted for aid to Dr W. Robyns, Director of the Botanic Garden at Brussels, Dr B. P. G. Hochreutiner, Director of that at Geneva, and Sir Arthur Hill, Director of that at Kew, at all of which places, and especially the first named, I have done much work. My friend Mr G. Udny Yule has helped me very greatly with criticism and assistance, and I am also much indebted for help to Mr J. S. Bliss, Dr C. Balfour Stewart, and many others.

J. C. WILLIS

LES TERRAGES
AVENUE DES ALPES
MONTREUX

25 March, 1940

CHAPTER I

THE COMING OF THE DARWINIAN THEORY OF NATURAL SELECTION

As a recent product of evolution, man must have arrived upon the scene to find himself in a world that was already well provided with animals and with plants. Some animals would be actively hostile and dangerous to him, some would be afraid of him, some would be indifferent; some plants would be poisonous, some good to eat or to provide useful materials, some indifferent. Man would presumably inherit some notion of what to eat, and how to obtain it, but it is clear that in his early days the struggle for existence must have been severe, especially if one remembers the prolonged infancy and helplessness of his offspring. He probably had greater brain power, and may have had some leanings towards co-operation, otherwise chiefly shown by insects. Whilst failure in the struggle for existence at the very beginning would probably have meant his complete extermination, the risk would lessen as he established himself in various different places removed from that in which he probably began. It is an intriguing thought that he may owe his first survival to having arisen in some place not troubled by dangerous animals, or to some other stroke of what seems like mere luck.

From very early times he must have been struck by the bodily likenesses of many of the organisms by which he was surrounded. He would soon recognise the difference between the male and the female of the same species, and he would distinguish, for example, between the tiger, the leopard, and the cat, or between the wolf, the fox, and the dog. He would see the evident likenesses that run through these triads, and that it was greater between tiger and cat than between tiger and dog. He would see other likenesses between goose, duck, and swan, between owl, eagle and hawk, or yet again between lizard, snake, and crocodile. But he would also notice that there were overriding distinctions among these various animals—that both the cat group and the dog group could be included in a greater group that we now call the Mammals, the eagle group and the duck group in the greater group of Birds, and so on. Thus there would grow up the notion of groups within groups, which is the essence of all classification.

The likenesses between plants are often less immediately obvious, and as compared with animals they seem to have been less remarked until a few centuries ago. One may see this lack of observation upon the part of mankind in the common names of plants, which are often old. Thus one often finds such names as meadow-rue, marsh-marigold, rock-rose, sea-heath, wood-sorrel, and the like, applied to plants that are in no way closely related to the rue, the marigold, the rose, the heath, or the sorrel, though they may have a superficial likeness in the leaves, in the look of the flowers, in their colour, or in the taste. But at the same time, one must also notice that many plants belonging to the same families (as now recognised) have similar names. Thus many Cruciferae, with their cress-like taste (cress itself is a member of the family), have names like bitter-, penny-, rock-, thale-, wart-, water-, winter-, and yellow-cress. The same taste, however, occurring in the seeds of the garden *Tropaeolum*, that plant used to be known as Indian cress, though it belonged to a totally different family. This also illustrates the now familiar fact that to place an organism in its proper relationships one must not rely upon a single character only. The name vetch is common among the British Leguminosae, and grass among the Gramineae, though here again one finds members of other families, often unrelated to the grasses, known as arrow-, cotton-, eel-, goose-, knot-, scorpion-, scurvy-, and whitlow-grass, because of some resemblance in habit, leaves, or other things.

Gradually the true likenesses of plants began to be recognised to such an extent that they were grouped into species and genera within families, and these again within larger groups, especially by the work of Tournefort, Linnaeus, Jussieu, Brown, Endlicher, and many others of more recent date, so that now we have what is probably a reasonably good classification of them.

Till about a century ago, the universally accepted view of the origin of plants and animals was that they had been specially created, each species in the form in which it now appears upon the earth, whilst their varieties were formed later, as the areas occupied by the species became larger or more varied. But it was clear that though one might group together the buttercup family, or the cat family, special creation would not explain, though it made the need of explanation greater, why they should possess such likenesses as caused them to be thus grouped together. Since the time of Aristotle vague ideas had been floating about,

that such groups might owe their origin and their likeness to descent from some common parent, accompanied by such modification in different directions that there would arise forms like the wolf and the dog, or the apple and the pear, showing an obvious family resemblance though differing in detail. But owing to the lack of any mechanism that seemed in any way capable of bringing it about, this idea of "evolution" was not seriously taken up, except by a few like Lamarck and St Hilaire, and never became what one may term practical politics until the coming in 1859 of Charles Darwin's famous book "*The Origin of Species by means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*", preceded, on 1 July 1858, by a joint paper by Darwin and by Alfred Russel Wallace, an independent discoverer, read at the Linnean Society. Both writers had been more or less inspired by reading Malthus (80) to realise the struggle for existence that must always be going on wherever living beings occur, a struggle which becomes the fiercer the more that they are crowded together, as for instance at the birth of young, or of germination of seeds, for it is well known that both animals and plants tend to produce more offspring than there is room for. Though by the aid of wind, water, animals, etc. the seed may be scattered to some extent, the chief crowd will always tend to be near together, and the great struggle will be among the seedlings, rather than between them and the parent, against which they will usually have but little chance. As there will generally be too many seedlings for the available space, the struggle will be severe, even if the competitors be connected with the parent by an offshoot or runner. The survivors will largely be chosen by chance, for early arrival on the spot, a less shady or better watered position, a better or softer patch of soil, and so on, will all be of greater advantage to the young seedling than any advantage that it may carry in itself as compared with its competitors of the same species, just as in the human struggle for existence parental advantage, the right school tie, etc. are of value. If it finds itself late in germination, upon poor soil, in a place with insufficient water, and so on, natural selection or competition will kill it out, inasmuch as it is unsuited to the conditions with which it has met, even though it may be suited well enough to what one may call the normal conditions of the place. It may also be killed out if it be the offspring of parents that have been used to somewhat different conditions, for it will probably carry with it their suitability to conditions. The more

like those from which it came that the conditions are, the better chance will the young plant have, whereas if it come from some distance, where the conditions are likely to be somewhat different, it will be more a matter of good luck should it succeed in establishing itself in the new locality.

As competitors begin to decrease, the struggle for existence will probably become somewhat less intense. When mature, the struggle will be largely that to secure the most of any small space for expansion of roots or of leaves that may become vacant.

Seeing a struggle like this, it seems natural to suppose that if any of the youngsters possessed any character that might give it any advantage against the rest, however slight, it would tend to win in the struggle more often than not. It is a remarkable thing that inasmuch as evolution is only clearly shown in structural characters, and natural selection was trying to explain evolution, it ignored the functional characters, and tried to explain the structural ones. But of course if the functional characters had been the only ones that were acted upon, there would have been little to show that any evolution had gone on at all. There would obviously be no need for all the structural differences.

Assuming that the advantageous character were inherited, another plant might win in the next generation, and so on, the character perhaps (another assumption) becoming more and more marked in each generation until at last, when taken together with other characters that had also varied (whether in correlation with the first, or also under the influence of selection), a specific difference was arrived at, and a new species would have been formed. As this would have been formed by a definite adjustment to the local conditions, it would be what is usually called adapted to them; this type of adaptation we shall call in future structural adaptation, as it was in structure that the changes were supposed to show that had brought the advantages with them. As it would tend to be the unimproved offspring of the old species, which retained its specific characters, that would be defeated in the struggle for existence, the old species would thus tend to decrease in numbers, being gradually reduced to the rank of a small and local group of plants, which might be looked upon as a relic of former vegetation, and which in time would die out altogether. And, supposing the original species to be found upon a considerable area, where there might be differences in conditions between different parts, then it might vary in two or more directions, giving rise to two or more species. In this case

the old species would tend to become discontinuous in its distribution by being replaced in some of its area by the new ones.

On the face of it, this suggested mechanism for the carrying on of evolution, to which Darwin gave the name of Natural Selection ("or the preservation of favoured races in the struggle for life") seemed eminently reasonable, and one that could do the work required. But the struggle was necessarily of each individual of a species for itself alone, and if one individual showed a favourable variation while its neighbours did not, the variation would soon tend to be lost by crossing. This was shown by Fleeming Jenkin (21) in a criticism which Darwin considered as the best that was ever made of his work. It therefore became necessary to stipulate for the same variation to appear in many more or less adjacent individuals of the species, scattered as a rule over a considerable area. Crossing would then be useful, rather than injurious. This in turn meant that the variation must probably have been controlled, directly or indirectly, by the external conditions, and these would most likely be those of climate or of soil, for the biological conditions largely depend upon which particular plants may happen to surround the individual concerned at any given place.

Instead of an external force, there might of course have been some compelling internal force which made a whole lot of individuals vary in the same way, and in this case one would certainly expect *all* to vary. Whether the force were external or internal, unless all varied alike over a considerable area, the advantage would be lost by crossing. In either case, it is a little difficult to see where natural selection got any leverage, for there would be no competition between the new and the old, except at the margin between them, where the new would in any case tend to be lost by crossing. When Darwin gave way, as he was forced to do, to this criticism of Fleeming Jenkin, the freedom of the natural selection theory was really lost.

The struggle for existence, felt as it was in every community and family, was such a commonplace of everyday life, that the principle had a very great psychological appeal, and was soon taken up on all hands. The long neglected theory of evolution rose "in the attitude of claimant to the throne of the world of thought, from the limbo of hated, and as many hoped, of forgotten things" (66). Rarely has any hypothesis met with greater success than did natural selection. A mechanism familiar to everyone seemed able to operate the long wished for process of

evolution. Every man felt, as Mrs Arber has said, that he was one of those picked out by it, and so he felt it his duty to support the theory. Though Darwin's immortal service was really the establishment of evolution, the name Darwinism became attached rather to the theory of natural selection, which became a cult, and which now exercises enormous influence in the world at large, even national policies being in some instances largely tinged with it. This is another instance of the influence of the dead hand, so well brought out by Woolf in *After the Deluge*, chap. i.

Evolution itself is now so well established that it has no longer any need whatever for any assistance or support from the hypothesis of natural selection, and whether the latter be true or not matters little or nothing. What we have to do is to follow up the theory of evolution, and find out something more about its working.

Natural selection was a new theory that was a complete reversal of the old. Instead of being created suddenly, so that at once they showed all their differences, which are often considerable, and usually more or less discontinuous, living beings were formed gradually by the selection and accumulation of small differences that gave some advantage to their possessors in the struggle for existence that was a daily commonplace of life. Creation in its usual sense was replaced by evolution, and the appearance of larger differences by the accumulation of smaller. The family resemblances that were mentioned above were now explained, thus removing to a period immensely farther back the conception that the phenomena of the life of animals and plants were pre-ordained, and throwing open to research a vast field of knowledge.

With natural selection itself, time has dealt less kindly. It acquired an immense prestige by its success in establishing evolution, but has not proved so useful in the further advance of science as was expected. It contains too many assumptions, and has required too many supplementary hypotheses to enable it to offer sure ground upon which to build, and is ceasing to be invoked as it used to be. It was at one time known as the doctrine of "nature red in tooth and claw", and as such has become largely incorporated into the theory of life that underlies the general policies of the world.

At the time of its greatest success, a rival, pre-Darwinian, system of evolution, known by the name of Differentiation, was

in process of development, and was being pushed by the famous zoologists Owen and Mivart. It must be admitted that against the psychological appeal of "Darwinism" it had no chance, but at the same time, there was even then much truth underlying it, and as time has gone on people are becoming more and more inclined to think that in some respects at any rate it will give a closer approach to the truth than will selection, the absolute need for which as a support for evolution has now passed by. Special creation went too far in one direction, natural selection in the other, and differentiation may be called a kind of compromise.

CHAPTER II

CONTACTS WITH DARWINISM. THE PODOSTEMACEAE

IT is not intended here to write a history of the movement known as Darwinism, but rather to sketch the author's contacts with it, which have lasted for fifty years.

The publication of the *Origin of Species* created a revolution in the world of science, but like most great changes in ways of thought it was very unwelcome to the older men, who rarely came round so far as to accept it in any whole-hearted way. In the next few years there was a flood of anti-Darwinian literature, and many incisive criticisms were made upon natural selection (rather than upon evolution) from one of which we quote the next sentence: "It follows, therefore, that if we accept the Evolutionists' view, every specialised chemical compound met with in some living beings only must fulfil the condition, that every approximation to the complete compound must have been of advantage to the being in which it was produced in the struggle for life...unless these very substances existed in, and formed points of difference between, Mr Darwin's few original forms" (29, p. 184). Maclaren also points out that change of climate does not change the chemistry of a plant, so that there is no opening for natural selection in a change of conditions.

It was clear that there must be discontinuity in evolution, and this was difficult to harmonise with the view that it had proceeded by gradual accumulation of minute steps. Chemical substances of differing nature could not be formed from one another by slow and gradual steps, nor could gradual steps in the formation of such a substance as the green colouring matter of plants (chlorophyll), for example, be of value. Yet this, probably one of the early formed organic substances, providing the food for plants and animals alike, ranks with water and protoplasm among the most important chemical substances in the world.

The writer has been chiefly occupied with economic botany for over forty years, and to him these considerations have long been a fatal objection to the current theory of evolution—the gradual passage, by reason of improving *structural* adaptation to the surrounding conditions of life, from small variations through

larger to well-marked varieties, to species, and to higher forms. There is no inherent reason why economic botany should remain what it now is, an ever-increasing mass of facts with little or no co-ordination. What little of this there is, as may be seen at once by consulting Wiesner's standard treatise, is very largely confined to such observations as that *a* and *b*, belonging to the same family, produce similar economic products. This alone shows that the facts of economic botany must be explicable upon evolutionary lines. Yet, with the exception of the theory that poisonous plants have evolved the poison as a protection against animals, natural selection has never attempted to explain anything in the realm of economic botany, which ought by this time to be a properly classified scientific discipline, with general principles running through it. One chemical fact must follow from another.

Something the same may be said of geographical distribution, which has been a favourite study of the author for the last thirty-five years. This again consists of a stupendous mass of facts, connected together by little more than a tissue of speculation. Sir Joseph Hooker, its great leader of former days, wrote: "All seem to dread the making Botanical Geography too exact a science; they find it far easier to speculate than to employ the inductive process", and the position is not so very different even yet. It has always been admitted that any theory of the mechanism of evolution must stand or fall according to whether it can or cannot interpret the facts of distribution. The two are obviously and inextricably bound together and to them should be added the facts of economic botany.

At first natural selection seemed to offer an explanation of these geographical facts, indeed so promising an explanation that Hooker became one of Darwin's chief lieutenants, never following out to their conclusions some of the lines of work upon which he had begun. Gradually, however, it was discovered that the employment of natural selection was not leading to real advance, and the first enthusiasm died away, leaving distribution in the Cinderella-like position that it still occupies. Those who had leanings in the direction of distributional study turned more and more to the rising science of ecology, known as natural history of plants when the author taught the beginnings of it under Sir Francis Darwin in 1891-4. But though ecology is all-important for the details of local distribution, it cannot answer the wide questions which are the province of geographical distribution.

properly so-called. Some new theoretical background is required, other than natural selection, which has proved a very broken reed upon which to lean.

Those who have tried to make evolution work upon Darwinian lines, i.e. in the "upward" direction from minute variety through variety and species, and so on, have met with continually increasing difficulties, with some of which we now propose to deal.

For the variations that were ultimately to form the basis of new species, Darwin relied principally upon the "infinitesimal" or continuous variation that was well known always to be going on in every possible character. Thus, supposing one measured the length of 500 leaves from similar plants of the same species, one might find the average to be 25 mm. The greatest single number would probably be found to show this length, but there would be almost, if not quite, as many measuring 24 or 26 mm., somewhat fewer for 23 and 27 mm., and falling away more and more quickly, but at about the same rate on either side. Investigation gradually showed that there were definite limits to this kind of variation. It follows the ordinary curve of frequency distribution. If one cross two individuals both having a very high degree of the character, the average of their offspring does not retain that high level, but falls back, or regresses. The high level can only be maintained by strenuous selection in each generation. Further, it is also found by experience that one cannot, by means of selection, pass a certain maximum. This kind of variation, in other words, is not fully hereditary nor is it irreversible, like the differences that characterise species, and cannot be indefinitely added up without some external aid. The experiences of sugar beet and other breeding show this well enough; never can one go beyond a certain point unless, by hybridisation or in other ways, one introduces new factors. In the struggle for existence, mere chance has much too large a share in determining the victors to allow even the maximum to be reached. Thus, on this ground alone, this type of variation was disqualified as forming an essential part of the evolutionary mechanism.

But this is not the only difficulty that arises in trying to use this kind of variation, which is always linear, or up-and-down. A leaf may vary infinitesimally in length, or in breadth, in the depth of its incisions, or in the degree of number and length of its hairs, but it does not vary except in sudden steps in such a direction as that from alternate to opposite, from simple to com-

pound, from pinnate to palmate, from dorsiventral (facing upwards, with different anatomy on the two sides) to isobilateral (facing sideways, like *Gladiolus* leaves, with the same anatomy on both sides), from parallel veined to net veined, or in other ways that could be mentioned. Now variations in length and breadth are rarely of much importance for distinction of species, unless so great that there is a wide difference between the averages in the two cases, while the other characters that have just been mentioned will be seen at once to be such as are of great importance in distinction between one species and another. This is another fatal objection to the use of this kind of variation as part of the mechanism of evolution. Some kind of variation was required that was not only inherited and irreversible, but also differentiating and not merely linear, or up-and-down.

Another serious difficulty was the fact that species were very rarely distinguished from one another by a single character only. Usually there were from two to six characters marking them off from one another, some of them more variable than the rest, and more liable to overlap from one species to the other, so that one had to examine a great number of specimens of each of the species to be sure that their overlap was not due simply to lack of real difference. Thus in *Cornus*, to take the first genus that comes to hand, *C. kousa* and *C. capitata* are closely allied species. The key division is that the former has the calyx truncate, the latter 4-lobed, and the involucral bracts more or less ovate as against obovate. But there are so many minor points of difference that the description of either takes up nearly twenty lines (49). None of the characters afford any opening for natural selection to work upon, so far as can be seen, but supposing that it had worked upon one, were all the rest simply correlations? One could hardly imagine it working upon one at a time, for what would ensure that *a* should be followed by *b*, which was unconnected with it (as are the two distinguishing characters above quoted)? Nor could one imagine it picking out a variation that included a little of each of *a*, *b*, *c*, *d*, etc., when these were unconnected, unless they were in some way correlated.¹ But if correlation were to be invoked to this extent, it must be the principal, though perhaps only passive, factor in evolution as shown by the characters that distinguish its finished product. Nearly all the

¹ Cf. *Origin of Species*, chap. vii, first few pages, for remarks upon this subject. Incidentally Darwin there suggests the "somewhere" which has proved such a useful refuge to the defender of natural selection.

characters must be correlations. And why did one not find, in the fossil records, any species that had been fossilised before this complicated process had been completed?

It is clear that, on the theory of gradual adaptation, a very long time must be allowed to get from one species to another. This means that the change of conditions must go on for a long time also, for if a small change in structure enabled the species growing in one locality to survive there, there would be no urgent reason why they should continue to vary in the same direction, unless the conditions also continued to vary in the same direction as that in which they had begun to do so.

Another difficulty was to understand why variations of this kind should usually go so far as to pass what one may call the rough-and-ready line of distinction between species—that they should be, mutually, more or less sterile.

One does not find to any serious extent in the fossil record, species which represent real intermediates between existing or fossil species. One finds rather examples of species that have some of the characters of one, some of another. But one does not find species (as from the constant occurrence of the few characters side by side in existing species one might expect to do) that show intermediate characters between alternate and opposite leaves, between palmate and pinnate leaves, between erect and climbing stems, between racemose and cymose inflorescences, between flowers with and without a cyclic perianth, between isomerous and heteromerous flowers, between imbricate, valvate, and convolute aestivation, between flowers with the odd sepal posterior and with it anterior, between stamens in one and in more whorls, between anthers opening by splitting or by teeth, valves, or pores, between 3-locular and 4-locular ovary, between ventral and dorsal raphe, between loculicidal and septicidal fruits, and so on through all the important structural characters.

All these were very serious difficulties, while it had also to be remembered that in any case evolution could only go on if the needful variations in the right direction should appear, for, unless this should happen, it was evident that natural selection could do nothing. One could not imagine the "mixed" variation of characters *a*, *b*, *c*, etc., above-mentioned appearing at all, unless most of it was simply correlation, and if the differences had to appear one by one, the chance of all appearing was but small, and the time required would be enormous. Forty years ago it was clear to the writer that some form of sudden and irreversible

variation was required, such as was supplied by de Vries' theory of mutation (48).

Evolution by gradual variation thus has many difficulties in its path, which in the first enthusiasm of natural selection were passed over with little notice. Under the influence of the criticism of Fleeming Jenkin, it had to be admitted that *all* the new plants of a considerable area must vary more or less in the same direction to prevent the new variation from being lost by crossing. It would be lost at the edge of its territory, but would presumably survive in the middle. The area of the parent species would thus tend to become more or less discontinuous. It had to be assumed that the parent did not vary in a favourable direction also, but as all variation was assumed to be structural (it could hardly be otherwise, as natural selection was trying to explain a *structural* evolution), it was easy to suppose that the parent could not vary in such a way. It also had to be assumed that the conditions continued to change for a very long time, to such an extent anyhow as to pass the sterility line, or a new species could not be formed. This new species would evidently be well adapted to the new conditions whose existence was responsible for its coming into being, but it had also to be assumed that when formed, or partly formed, it would then prove so suited to the region in which the parent was still supreme as to kill out the latter there also. This was a pure assumption, but was necessary in order to explain the spread of the newer and better-adapted species, which in turn was to explain their wide distribution. We have shown in *Age and Area*, p. 34, that the older species will probably gain continually upon the younger in rate of dispersal, supposing, which seems to be the case, that there is no reason (when they are taken in groups) why one should spread more rapidly than another nearly related to it. If the area to which the new species was ultimately to reach were very large, it was really rather absurd to talk of it as adapted to the whole area. It must have been just a case of luck that it proved so sufficiently suited to far-away places as to be able to establish itself there, though once arrived it would begin to suit itself in detail to the local conditions. And it must not be forgotten that early species would have the best chance both of rapid travel and easy settlement.

Finally, among the difficulties of Darwinism, it was evident that the variations must be such that natural selection could work upon them when they did appear, and as to that we have but little evidence.

The hypothesis of evolution by small variation has never, so to speak, been officially abandoned, but it has been so altered by supplementary hypotheses that it is hardly recognisable, and the theory of mutation, brought up by de Vries, has largely taken its place. A mutation, which when obvious is often called a sport, at once produces a morphological or structural character or characters that are definitely distinct from those which were found in the parent form, and not only that, but which have come to stay, and are (practically) irreversible. It is always possible, of course, though not very probable, that some later mutation may change them, or some of them, back again, or to something else. Here, then, was a hypothesis that surmounted the chief difficulties mentioned above, and provided hereditary variations that were differentiating and (practically) irreversible.

Mutation was taken up, though slowly, as people gradually realised the fatal nature of the objections to linear and infinitesimal variations. Unfortunately for its speedy success, some doubt was thrown upon the genuinely mutational nature of the phenomena upon which it based. Some, at any rate, appeared to have been due to hybridisation. But in spite of this setback, mutation had come to stay, and we shall trace some of its history below. People say that a sport is not capable of succeeding by itself, but we do not know what would happen if it were really viable, and plenty of *time* were allowed.

- ✓ Natural selection was, of course, essentially a theory of gradual, progressive, and more or less continuous adaptation to surrounding conditions. It is evident that living things are suited to them, for if they were not they would soon be killed out in the struggle for existence. Some theory that will explain adaptation is, therefore, very desirable. It was largely because it seemed so capable of doing this that natural selection was so enthusiastically taken up.

Each new species was formed, according to Darwin, because it was an adaptational improvement upon its immediate ancestor. Once this was fully realised, there was a great rush into the study of adaptation. It was taken for granted (it could hardly be otherwise) that as natural selection was trying to explain evolution, which showed itself mainly in external structural characters, these characters must also, of necessity, be the means of expression of adaptation. Evolution has undoubtedly gone on in morphological change, but as yet we are practically without any proof that the change also represents the adaptation that may

have gone on. What natural selection undoubtedly does is to work with the individual, and to kill out, upon the whole, those individuals that are below the average in any species—man or animal or plant—but we have no proof that it works in the same way with species as a whole or as units, killing out one species or variety to make room for another, unless in particular conditions which are more or less local. A species *a* may be killed out in one place, because of unsuitable local conditions, whilst its rival *b* may be killed out in another, for the same reason. If structural differences go for anything, there must be a great adaptational difference between the Dicotyledons and the Monocotyledons, yet both grow intermingled almost everywhere, and in much the same proportions. There is no “monocotyledonous” mode of life that suits a Monocotyledon better than a Dicotyledon, yet there are very great structural differences between them.

During this period, the possibility of internal, functional, or physiological adaptation was ignored. Yet adaptation has far more to do with the physiological than with the morphological characters, if indeed it has anything to do with the great bulk of these. There are very few external characters to which one can point as definitely physiological. The leaves, roots, stems, flowers, and fruit are so to a great extent, but not *differences* in these (such as palmate or pinnate leaves, or drupes and berries), except rarely. Adaptation to climate, which is a physiological difference between one form and another, is primarily a purely internal adaptation. To have any chance of survival, a species must be suited to a greater range of climate than that with which it perhaps began. As it migrates into new territory, it will probably begin to become adapted to the slight changes with which it may meet as it moves with (usually) very great slowness into slightly differing conditions.

A vast amount of energy was put into the study of adaptation during the last quarter of last century, and the imagination was pushed to the extreme limit to find some kind of adaptational value in even the least important features of plants, such as a few hairs in the mouth of a corolla, an unpleasant smell (to some human beings), and innumerable other characters (cf. books of this period, such as 23). Unfortunately for the adaptationist and for the theory of natural selection, which was founded upon adaptation, no one was ever able to show that the important morphological features of plants, which showed so conspicuously in the characters that marked families, tribes, genera, and most

often also the species, had any adaptational value whatever, and the higher that one went in the scale, from species upwards, the more difficult was it to find such a value. This, when one comes to think it over, is really a very puzzling fact—*why* should the differences become larger the higher one goes? Is the struggle for existence greater among the higher groups, between two families for example, than between two species, and between these than between two individuals? A glance at the table of family characters, given as Appendix I, will illustrate this.

This list of the important characters that distinguish families from one another is after all not so very large. Each family has something to show under most heads. In any pair of allied families that may be taken, there will be mutual agreement in many characters, but a contrasting difference in others, one character of a pair being taken in preference to the other, and that character tending to be shown right through the family, though there are nearly always exceptions in the larger families, the number of exceptions tending to rise with the size of the family. Most of the pairs of characters that are given are such that they do not admit of intermediates, and this *divergence of variation*, as it is called, is constantly to be found in nature between organisms that are so alike in most of their characters that they are evidently allied in descent. Divergent differences may show between one species and the next, between one genus and the next, as with the berry-fruited *Cucubalus* in Caryophyllaceae, between one tribe, sub-family, or family and the next. As one goes downwards in the scale from family characters, one finds more and more characters coming into use, but they can still very often be arranged in divergent pairs.

One does not find (usually it is impossible) intermediates between the two characters of a pair, except in a few like superior and inferior ovary, where semi-inferior is possible. But to imagine intermediates between alternate and opposite leaves, or between most of the pairs given, is to ask too much of selection. These characters must, one would imagine, be the result of some sudden change, which would give one or the other.

The individual characters are so divergent from one another in each pair that it is clear, as in fact has long been well enough known, that variation is definitely divergent. This was always, as Guppy has said, a worry to Darwin, for it was extraordinarily difficult to understand how an evolution, working "upwards" through the variety and species, could drop out at each stage the

organisms necessary to make the divergence show more and more as one went up in the scale. As Guppy points out in *Age and Area*, p. 104, Hooker was definitely considering the idea or nucleus of a theory of differentiation (19, II, 306) but "no inductive process based on Darwin's lines could have found its goal in a theory of centrifugal variation.... Huxley was in the same case. For he held views of the general differentiation of types, and his road that would lead to the discovery of the causes of evolution started from the Darwinian position. That road was barred to him."

One cannot conceive of any of these family differences being formed under the influence of natural selection. One cannot even suggest, in any single case, which of the two characters is the earlier, or what advantage can be gained by one as against the other, or as against any possible intermediate, if such a thing could exist at all. One must also remember, in dealing with natural selection, that there must have been an enormous destruction of intermediates, of which we find no fossil record of any note.

The supporters of natural selection mostly (at present, that is, for they are apt to change over to the reverse explanation, that of local adaptation) look upon the small and local genera and species which occur in such great numbers, as being the losers in the struggle for existence, i.e. the relics of a former vegetation, now upon the way to extinction. A very remarkable thing about these relics, which they do not attempt to explain, is that they do not occur, except very rarely, in two or more different localities, with a wide separation. For example, there are hardly any cases known where they occur in two different continents, and few where they are found in the interior of two different countries on one continent. Nor do the great majority of them belong to small and isolated genera, but to the large genera (cf. p. 26), which natural selection regards as the successes. The "relics" therefore must have belonged to ancestral species which must have been widely distributed to give rise to their present descendants. Why then, when in one or more regions of slightly different conditions new species were developed, did not the old species become discontinuous in its distribution, leaving relics in several different places?

Under the natural selection theory, the large genera in the big families, like *Senecio*, *Ranunculus*, or *Poa*, are supposed to have been the best adapted and therefore the most successful. But

they are worldwide in their distribution, which must therefore have gone on in early times. Has natural selection been gradually diminishing in its effects?

The characters given in the "family" list are very important in the distinctions between families, but they also appear very frequently in distinctions between tribes, less often between allied genera, and still less often between two allied species. It is evident, therefore, that they can be rapidly produced, and do not necessarily need a long and gradual evolution from species upwards. It is difficult to see how this can be so, unless they can be the subject of single sudden changes, which as they are usually divergent is not difficult to imagine.

It is very difficult to apply the Darwinian explanation, that distribution is due to superior adaptation, to a genus like *Senecio*, for most of its species are, compared to the genus, quite local. If there be any marvellous adaptation, then, to account for the enormous distribution, it must be generic, and no one has ever been able to make even a suggestion as to what it may be, or wherein it is shown. The generic characters are purely morphological, with less functional adaptation even than the specific.

The writer, as personal assistant to that best and kindest of men, Sir Francis Darwin, who had helped his father in so much of his work, was, of course, brought up in the arcana of natural selection, and accepted it with enthusiasm. His first research was upon adaptational lines, but he was not satisfied with the adaptational explanation of things, and when soon afterwards, in 1896, he went to Ceylon to succeed Dr Trimen, his views underwent a complete change. The leisure time of the first six years was devoted to a detailed study in both Ceylon and India of that remarkable family of water plants the Podostemaceae (51-55), containing about forty genera with 160 species, found in all the tropics, with overlap into cooler regions. All live upon the same substratum of water-worn rock (or anything firm, like timber, that may be caught in the rock) in rapidly flowing water. They are annuals, flowering immediately that the spathe comes above water in the dry season, and then dying. If accidentally laid bare by an unusual fall of water in the vegetative season, they soon die without flowering. All the food comes from the water, and they have no competition for place, except among themselves. Enormous quantities of minute seed are produced, which have no adaptation at all (except in *Farmeria*) for clinging to their place in the swift current. At most one in a thousand or two may be

caught in some fragment of old plant, or in some other place where it can germinate.

At the period when this study was undertaken, the Podostemaceae, with their strange look of lichens or seaweeds, their peculiar mode of growth, their great variety of form, were looked upon as obviously showing adaptation in the highest degree, and it was for this reason that the work was undertaken. But among the conclusions drawn from it was this, that apart from those adaptations which they showed in common with all water plants, such as the lack of strengthening tissues and of stomata, there was in them little evidence of any special adaptation whatever. The conditions under which they lived were the most uniform that it was possible to conceive—the same mode of life, no competition with other forms of life, the same substratum, the same light (varying from day to day with the depth of the water), the same temperatures, the same food, everything the same. Yet in spite of this, the plants showed an enormous variety of form, greater than that of any other family of flowering plants whatsoever, while water plants as a rule show little variety in form, and have but few genera and species. Still more remarkable was it that their morphology differed for each continent, flattened roots in the Old World, flattened shoots in the New, so that it was usually possible to say by a simple inspection what was the probable habitat of a species never seen before. It was hard to believe that natural selection, working upon structural modifications that have never been shown to have any functional value, could do this. The linking genus, *Podostemon* itself, covers an immense area, including that of many of the smaller genera, and is less dorsiventral than they are, though all show a highly dorsiventral flower, which stands erect, and is commonly wind pollinated, an unexpected combination of characters for the selectionist to explain.

Once these very remarkable facts were fully realised, the explanation that seemed much the most probable was that on the whole the highly dorsiventral genera were descended from *Podostemon* or from some form like it. It could not be the other way about, for the flowering plants as a rule are not dorsiventral, except in the structure of the leaf, and very often in the flower. Nor could there have been some intermediate form, for that would have had to be more dorsiventral than are the flowering plants in general. One only of the local genera, *Willisia* in the Anamalai mountains in South India, shows as much ordinary

symmetry in its shoots as *Podostemon*, and as in that genus they grow adventitiously from a creeping root.

The plants of this family grow in conditions of uniformity that can hardly be matched in any other flowering plants, but amongst them is included the uniform action of a force which cannot be escaped. Growing as they do, always upon smooth water-worn rock, they *cannot* send their roots into the substratum, so that the normal polarity of the young plant, which sends its root down and its shoot up, is completely disturbed. By no contortions can the plants grow normally, though the rock may be of any kind of slope.

There was no evidence to be found that would show that natural selection had anything to do with the multiplicity of form in these plants, for all were growing under the same conditions; but there was always this inescapable force urging dorsiventrality. Under these circumstances, though he had started out with great faith in adaptation and natural selection, the author became a convert to the theory of mutational origin of species, adopting from the very first the view that mutations or sudden steps might at times be large enough to form species at one stroke. There were no signs of real intermediates, yet surely here if anywhere they might have been expected. An ordinary plant of another family, growing more or less vertically upwards, would not usually come under the continual influence of any powerful agent which would tend to make its mutations go in any particular direction, but with the Podostemaceae they were always being pushed in the direction of dorsiventrality by the maximum force that nature was capable of exercising in that direction. The mutations of ordinary plants would give rise to specific differences in which one could see no result of any particular directing force—there was little or nothing to choose between them, and they were morphological differences, with no adaptational value. In the Podostemaceae, on the other hand, the mutations showed the result of the continual force that was acting upon them, in a dorsiventrality that on the whole tended to be continually more and more marked the more local the genus might be. But it was only an adaptation in the sense that moving restlessly in bed might be described as adapting oneself to wearing pyjamas of the fabric of which hairshirts were made. The dorsiventrality was simply a morphological feature which had been forced upon the plants. Upon this view, the difference in morphology between the American and the Asiatic forms was also easily accounted for

by some small difference in morphology between the first parents in the two countries, which had the effect of urging the first mutations in somewhat different directions. It is, of course, true that natural selection might do the same with the same start, but it is not quite so easy to imagine.

Any member of the family seems to be able to live without any great difficulty where any other member can live (53, p. 535) though probably they have some preference as to speed of water, and one must remember that in any case this varies with the level of the river, being usually faster the higher the level. People who came with me to look at the Podostemaceae growing in the river near Peradeniya, when they saw the flat, closely adherent *Lawias* or *Hydrobryums*, used to say "obvious adaptations to escape being carried away by the fast water". But in Brazil the comparatively enormous *Moureras* and other forms, 3 or 4 ft. long, yet attached only at one end, lived in water that was going at twice the speed of that in Ceylon.

Much or most of the evolution that had gone on, therefore, seemed to be completely *de luxe*, for there was no need for the new forms, nor was there any adaptational niche that would suit one form only, and not also many others. It would almost seem as if, in cases like this, if not perhaps in most, *evolution must go on, whether there be any adaptational reason for it, or not.*

The explanation of the distribution of the Podostemaceae, as given by current theories based upon natural selection, encounters some awkward difficulties. The most highly dorsiventral forms are the most local, i.e. they are "the relics of previous vegetation, defeated by the more widely distributed ones". In other words, the family began with extreme dorsiventrality, and then, so to speak, repented of it to some extent. But to become less dorsiventral under the constant and utmost influence of a force that is urging movement in the opposite direction, can hardly be looked upon as likely to happen under the influence of natural selection and the whole situation becomes an impasse.

The phenomena shown by the Podostemaceae are almost exactly matched in the allied family Tristichaceae, which has much the same distribution, and are also matched by the phenomena shown by the most completely parasitic plants, such as Rafflesiacae or many fungi, which, though they grow in marvellously uniform conditions, none the less show important structural differences.

The universality of this type of distribution, with the more

primitive genera the more widely distributed, and the most highly modified the most local, taken together with other features shown by the Podostemaceae, made the writer realise that in trying to work evolution from the variety—which upon the theory of natural selection was an incipient species—upwards to species and further, we were trying to work it *backwards*. Once this fact had been fully grasped, as it was about thirty-five years ago, the theory of natural selection became for him a theory which in its youth had done a marvellous piece of work, but had exhausted itself in that effort, and was not likely to lead to any further serious advances, as indeed had already been shown in its breakdown in the study of adaptation in the last quarter of the nineteenth century.

During the six years that this work occupied, the writer had frequent opportunities of visiting the tropical forest, and soon realised that the struggle for existence was mainly among the seedlings that tried to commence life upon any small spot upon which, owing to fall of a tree, the breaking off of a branch, or for other reason, there was rather more light than usual. But most of the seedlings were of differing species, and commonly also of different genera. And as never twice would the same assortment of seedlings have to be encountered, and never twice the same conditions of weather, it was impossible to see how slight variations towards adaptational advantage could be of any use. Mere chance, as we have already pointed out (p. 3), must evidently be the chief factor in determining the survivors. Ecological adaptation to slight climatic and other changes must evidently be internal rather than external. It was possible, as Harland has suggested, that slight changes of this kind might entail some genic change, and these, when added up over long periods, might give rise to morphological mutations. But this has little or nothing to do with the straightforward natural selection that was normally accepted, and in any case is working downwards from above, as does differentiation.

The fiercest struggle for existence that a plant is ever likely to encounter is that into which it must be thrown at its birth, when it will have to compete with other seedlings upon land already very fully occupied. Any form that is not adapted to the conditions in which it finds itself *at that time* will be remorselessly killed out, unless the time is short, *by reason of its unsuitability*, and that is what natural selection really means. Anything that is in any way handicapped—*by unsuitability to the conditions*,

by anything unfavourable in the spot upon which it is trying to grow, by mere late arrival as compared with its competitors, and so on, cannot survive in such a struggle, unless the handicap imposed by one thing is compensated by a start in some other. The actual winner or winners will be mainly picked out by chance, and will in all probability be derived from parents that are already living somewhere close by, and which may therefore be looked upon as already adapted to the climate and other conditions. In all probability this adaptation will be to a reasonably large range of temperature and other climatic conditions, for unless this were so, survival would be very improbable in most places. There is also reason to suppose, that if it be done slowly enough, a species may, as it moves slowly about the world, become slowly acclimatised to other conditions, for the range of some species is so enormous, and includes such varied conditions, that without some possibility of this kind it is difficult to understand.

CHAPTER III

CONTACTS WITH DARWINISM, *continued.* ENDEMISM, AGE AND AREA

HAVING by this time (1902) completely thrown over natural selection as the chief mechanism of evolution, the author's next piece of work was a study of the remarkable flora of Ritigala mountain, lying isolated in the flat "dry" zone of Ceylon, in which little or no rain falls for the almost six months of the southwest monsoon. A note on the flora had already been published by Trimen (45). The mountain, over 2500 ft. high, falls with a steep cliff to face the south-west wind, and the summit, of but a few acres, receives rain during that monsoon, thus forming an outlier of the "wet" zone flora, which otherwise only begins upon the mountains about 40 miles away to the south.

The flora of Ritigala summit, of over 100 species, contains one or two which are quite local to it, or *endemic*, in the botanical sense. The rest of the plants are largely to be found in the wet zone, but not in the intermediate country, which is at a much lower elevation, and is shown by geological evidence probably to have been dry since the Tertiary period.

Endemism, about which the writer has published a good deal of work, is, it is hardly too much to say, a crucial feature upon whose proper explanation largely hangs much of the whole matter of evolution and of geographical distribution. The best known endemic of Ritigala is *Coleus elongatus* Trim. (46, and Plate 74), easily distinguished by having a calyx of five equal sepals instead of one of two lips, and by having a pendulous cymose inflorescence of five stalked flowers, in place of the sessile bunch of five flowers that is the usual thing in Labiateae. There also occurs upon the summit the closely related *C. barbatus*, widely distributed in tropical Asia and Africa, and upon the natural selection theory the most "successful" of all the *Colei*, but here growing together with *C. elongatus* the most "unsuccessful", and in the same way, upon open rocky places. Why was this so, upon the hypothesis of natural selection? No satisfactory answer could be given by its supporters, and they were obliged to bring in two supplementary hypotheses, which were mutually contradictory. Some said that

C. elongatus was a local adaptation, i.e. a success, but if so, why did it not have a different habitat from *C. barbatus*? Others offered the reverse explanation, and said that it was a relic of previous vegetation, i.e. a failure. But again, why did it continue to grow in the same places as *C. barbatus*, the most widespread and successful of the *Colei*? Why was it not killed out? And why was it morphologically distinct from all other *Colei*, with a few exceptions in Africa? Had a pendulous inflorescence with stalked flowers given rise to a normal Labiate one, which otherwise characterises much of this genus of 150 species of tropical Asia and Africa? And how did the calyx change from five equal teeth to two lips, one presenting four teeth, one one? Regular variation in a calyx would always affect the teeth equally; a two-lipped condition could only be the result of some sudden change. The final refuge of the natural selectionist is usually to say that the peculiarities must have been useful at some other time, or at some other place. But the conditions upon the summit of Ritigala, and in all probability in the country between it and the wet zone, had not altered since the Tertiary, and there was no sign of *C. elongatus* anywhere else, while its most successful and closely related rival, *C. barbatus*, was upon the same summit, in similar places, and about equally common. Neither of the diametrically opposed solutions offered by the natural selectionists would hold water, especially as no adaptational value could possibly be read into either inflorescence or calyx, whereas the problem was easily solved by imagining *C. elongatus* to have arisen by a single mutation from *C. barbatus*. And why was there another endemic in the mountain mass of the wet zone also? Was it a case of isolation resulting in a new species upon Ritigala? This was the only probable explanation other than that of mutation which has been offered, and as the wet-zone endemic has neither the equal sepals nor the pendulous inflorescence, marked mutation must have gone on. There was no opening for natural selection, even could it have produced such differences among the few dozen plants of both species upon the summit of Ritigala. It was also clear that upon the principles of natural selection, as altered by Darwin after the destructive criticisms of Fleeming Jenkin (21), there was not room enough upon the summit of Ritigala to allow of the development of even one endemic, to say nothing of two or three, or of the surprising fact that the most common and widespread species of *Coleus* was also living there with the local endemic, and in the same or similar places.

This work fully confirmed the author's doubts concerning the efficacy of natural selection, and the weakness of the explanations that were put forward in its name. He also became interested in endemics for their own sake, for it was becoming evident that upon a correct explanation of them depended much of the proper understanding of what had gone on in the course of the evolution and geographical distribution of plants that had occurred in the earth's past history.

Work upon endemism has been continued ever since the first experience upon Ritigala, and has led to many interesting results, many of which were published in a book upon *Age and Area* in 1922, and others of which it is hoped to publish in another book dealing with Geographical Distribution only. One of the first interesting points to come out was the very great number that were confined each to one (or more rarely to two or more) of the mountain summits of Ceylon (57). It was shown that over a hundred species were confined to one or more hill-tops. Thus the large tropical genus *Eugenia* showed *E. Fergusonii* and *E. aprica* in the mountains north-east of Kandy, *E. cyclophylla* and a variety of *E. Fergusonii* upon Adam's Peak, *E. phillyraeoides* upon Kalupahanakanda, *E. pedunculatus* in the Rangala mountains, and *E. rotundifolia* and *E. sclerophylla* upon the peaks above 6000 ft. The mountains, all rising from a plateau, thus had eight peculiar *Eugenias*, which one could not figure as being refugees from the plains by way of the plateau (an explanation sometimes advanced). They also contained six endemic *Hedyotis*, ten *Strobilanthes*, four *Anaphalis*, and so on. Plants like this are usually supposed to be relictives of previous vegetation and it was of special interest to notice here what in fact is generally the case throughout the warmer parts of the world. The nineteen genera that show more than one mountain endemic are represented in Ceylon by 268 species, or 14 species per genus against an average representation of 2·7 species, and in the world as a whole these genera contain 4095 species, or 215 per genus, against an average of about 18. They are thus not only very large genera but also genera that make up nearly 10 per cent of the whole flora of Ceylon, and 2 per cent of that of the world. And this is the general rule with regard to endemics, wherever they may occur.

It looked as if there must be some definite reason for the commonness of endemics upon mountain tops, and I suggested cosmic rays, though mere isolation might be sufficient.

The mountains of Ceylon thus behaved, in regard to endemism,

just like the separate islands of an archipelago, where again the endemic species behave in this manner, belonging to large genera, with a distinct tendency to differ among themselves upon the different islands. It was, therefore, concluded that there was nothing peculiar in the existence of an oceanic island that should give rise to endemics, other than the qualities that it shares with mountain tops, which show like islands in their possession of local species. "Of these the most obvious is isolation, and we may, I think, justly draw the conclusion that has often been put forward, and say that isolation, *as isolation*, favours the production of new forms" (57).

The study of endemism begun in Ceylon was recommenced at Rio de Janeiro early in 1912, and soon led to the hypothesis of age and area about which many papers and a book (66) were published in the following ten years. By the courtesy of the Editor of the *Annals of Botany* I am allowed to quote, with modification and omission, from a paper of 1921 (65) a short summary then written:

Examining on many occasions, from 1896 onwards, the... *Flora of Ceylon* (46),... I gradually found, somewhat to my surprise, that the strictly local species confined to that island, or *endemic* species, as we usually call them, which are very numerous in Ceylon, showed on the average the smallest areas of distribution there, whether in the grand total or in individual families (cf. 70, p. 12). On the older view of the meaning of endemic species, which I then held, this seemed a very remarkable thing—that species which were generally looked upon as having been specially evolved to suit the local conditions should be so rare in those very conditions. If these species were specially adapted to Ceylon, therefore, it could not be to the general conditions of the island, but must be to strictly local conditions within its area. There was clearly no difference between island endemics and those of the mainland. Accordingly, still more remarkable did it seem when I came to study in detail the local distribution of these endemic species in Ceylon, and found that, as a rule, they were *not* confined each to one spot or small region characterised by some special local peculiarity in conditions, to suit which they might have been supposed to have evolved. Not only so, but such spots were frequently to be found with no local species upon them. Only about a quarter of the whole number were confined to single spots, and more than half of those were restricted to the tops of single mountains (57). The remaining three-quarters occupied areas of larger and larger size, and in diminishing numbers as one went up the scale.... The very rare species are as a rule well localised, but the rare and rather rare... cover areas

that *overlap* one another like the rings in a shirt of chain mail. Now a little consideration will soon show that from the point of view of evolution to suit local conditions this is a very remarkable state of affairs. If *A* and *B* grow in overlapping areas, both must be growing in the coincident portion, and what keeps *A* from growing into the rest of *B*'s territory, *B* into *A*'s? In reality the case is more complex, for if all the species were entered, there would be... a dozen overlapping at any one point. It is all but inconceivable that local adaptation should be so minute as this, with soil essentially the same throughout, and the rainfall, etc. varying much from year to year. The species would have to be adapted to wide range in rainfall, and to very slight in a *combination* of other factors. It was clear that the old ideas of particular adaptation were quite untenable.

Nor would the other popular theory, which equally survives to-day, satisfy the knowledge that I now had about local distribution. How could species be dying out in this remarkable chain-mail pattern, and why were there so many with small areas? Had one perhaps arrived in Ceylon just in time to see the dying out of a considerable flora? And why did so many choose mountain tops as a last resort? If they had climbed from below, they must have plenty of adaptive capacity, and should be able to compete with the new-comers. Still more, why did each one or two choose a different mountain?... It was difficult to believe that the plains were once inhabited by different species at every few miles, whilst many mountains with endemics did not even rise direct from the plains, but from a high plateau.

Counting up all the species of the Ceylon flora, and dividing them into three groups—those endemic to Ceylon, those found only in Ceylon and South India, and those with a wider distribution abroad than this (which I termed *wides* for short)—I found (59) the endemics to be graduated downwards from few of large distribution area to many of small (e.g. common 90, rare 192), and the wides in the other direction (e.g. common 462, rare 159), with the Ceylon-South India species intermediate. In other words, the average area occupied by an endemic was small, that by a Ceylon-South India species larger, and that by a wide the largest of all. A cursory examination of other floras showed me that their endemic species also behaved in the same way,... and I was at last furnished with what seemed to me to be a much more feasible explanation of the distribution of species in general, and endemics in particular.

Having disposed, to my own satisfaction, of the notion that endemics were moribund species, I adopted the view that in Ceylon the wides were the first species (*on the whole*¹) to arrive, and had therefore on the whole occupied the largest areas. The Ceylon-South India species, on my view, must have arisen from

¹ I.e. in any genus the wide would usually be the first to arrive.

them at points in general south of the middle of the Indian peninsula, and would on the whole be younger in Ceylon than the wides, and therefore occupy lesser areas on the average. The Ceylon endemics would arise from the wides (or Ceylon-South Indians) in Ceylon, and would be the youngest, and on the average occupy the least areas. All the figures of course must be worked in averages, for an endemic of one group might be occupying a large area when the first wide of another arrived.

Confirmatory evidence was soon obtained from the floras of New Zealand, Jamaica, Australia, and the Hawaiian Islands. The figures for New Zealand are as follows:

Range in N.Z.	Wides	Endemics
881–1080 miles	201	112
641– 880	77	120
401– 640	53	184
161– 400	38	190
1– 160	30*	296

* Largely undoubted introductions of recent years.

Facts like these, which are universal, cannot be the result of a selection, but must have some more mechanical explanation. The only one that to the writer seemed at all satisfactory was simply *age*, as was explained in *Age and Area*, though of course age in itself was not exactly a factor in distribution. There are very many factors that may affect dispersal, but if one suppose factor *a* to produce an effect in distribution in a long time *x* that may be represented by 1, one may reasonably expect that in time *2x* it will produce an effect 2. If the effects of all the factors be added up, the total effect in time *x* may be represented by *m*, and in time *2x* by *2m*. Obviously there will be great individual differences between species, so the proviso was made that *comparison* (with a view to determining questions relating to age) must only be made between *allied* forms, which were most likely to behave in an approximately similar way under similar circumstances. The quickly reproducing, herbaceous Compositae must only be compared with other Compositae, not with the slowly reproducing trees of the Dipterocarpaceae or the Conifers; and so on. One form might even occupy in a decade what might take the other several centuries to occupy. And not only must this precaution be taken, but closely allied species, even, must be taken in tens, to allow of averaging the effects of the many factors that might take part in their distribution. But, bearing these things in mind, one might say that large area of distribution

meant considerable age, small area small (each set of plants compared being taken from the same circle of affinity).

And also, one must always remember that the distribution of plants is very largely controlled and determined by the presence or absence of barriers, which may be of many kinds. There may be simple physical barriers like the sea, or a mountain chain; there may be the barrier of a climatic change from warm to cold, or from dry to wet, and so on; there may be ecological barriers imposed by the habit or other peculiarities of the plant itself, and so on. The whole question is discussed in detail in chap. v (p. 32) of *Age and Area*.

So axiomatic did all this seem, that the author was somewhat surprised by the vehement opposition that it encountered. The explanation of this perhaps lies in the fact that geographical distribution would thus be transferred to a more mechanical sphere than had hitherto been allotted to it. No longer, especially in view of the regular arithmetical arrangement, could the natural selection theory supply a full explanation of the facts of evolution into genera and species, and no longer, in face of the fact of increase in number downwards in the case of endemics, upwards in case of wides (table on p. 29), could it supply a full explanation of the facts of distribution, or of the nature of endemics. Sooner or later, it seemed to the author, these new discoveries meant that natural selection, in its present form at any rate, would cease to be so important a factor in evolution, and with evolution of course went distribution and many other branches of biological science.

One of the most important things that would necessarily follow from the acceptance of age and area was the replacement that it asked of the long-cherished notion that endemics in general were either relic forms, or local adaptations, by the supposition that when they occurred in very small areas they were mostly young beginners as species, that had not yet had time to occupy larger areas. In many cases of course barriers (especially barriers due to climatic or soil conditions) that would in any event obstruct or prevent further spread were so close that only small areas could be covered, even though the species might be very old. Other species, again, of very limited distribution, and that more especially in the north within reach of the effects of the cold of the last glacial periods, were evidently relics. Sinnott (*Age and Area*, p. 86) gives, as examples of this class in North America, *Carya*, *Planera*, *Maclura*, *Garrya*, *Sassafras*, *Xanthorrhiza*,

Baptisia, *Nemopanthus*, *Ceanothus*, *Dirca*, *Dionaea*, *Hudsonia*, *Rhexia*, *Ptelea*, *Decodon*, *Houstonia*, *Symporicarpus*, etc., many of which are fossil in the Old World. As they also include most of the woody endemics of North America, and as each of them belongs to a different family, it is highly probable, if not certain, that they are relics. But, as already pointed out, they are lost in the crowd when considered in connection with their own families, especially as most of them are but small genera. And though they may be relics of a previously more woody vegetation of North America, we have no reason to suppose that they are being killed out by superior species—they have probably been much reduced by change of climate and are not quite so well suited to the conditions that now exist. In warmer countries one comparatively rarely finds endemics of this kind; the endemics, as has already been pointed out (*Age and Area*, pp. 91, 165; and p. 26 above), occur chiefly in the large and “successful” genera, like *Ranunculus* or *Poa* in New Zealand, or *Eugenia* in Ceylon or in Brazil.

Among these just quoted relics there occurs *Ceanothus*, with forty species in North America only, a genus that must be counted as large for that country. In a recent discussion, *Artocarpus*, the jak and breadfruit genus, which is the third largest genus in the large family of the Moraceae, and has over sixty species scattered over Indo-Malaya and China, was quoted as a relic, on the ground of the occurrence of fossils outside its present area. This kind of definition of relic seems to the writer something of a begging of the question. We can no longer be sure that any plant is not a relic. The whole British flora must evidently consist of relics, except perhaps the very local species farthest from the land that has been submerged, and yet the flora is in reality a very young one in its present position. If a change of conditions affect a country, it is in the highest degree improbable, except in a case like the coming of the ice, that it will kill out *all* the former flora—it will be gradually and partly replaced by newcomers that better suit the newer conditions, and if the conditions change back again, these may be in turn replaced by the older flora, and gradually things may become much as they were before the first change.

One reason, perhaps, for the unpopularity of age and area was the realisation that it was incompatible with the current view of the way in which evolution had gone on. If we follow it to its logical conclusion, it is clear that as the family in general occupies

a larger area than the genus, the genus than the species, the family must be the oldest, or (where, as is often the case, one genus covers the family area) as old as its oldest genus. This turns the Darwinian theory upside down, for upon it the family is a later appearance. There is, however, no evidence for this. However far back we go in the geological record, we always find families that are identical with some of those of the present day. They are also usually widely separated, so that even at that early period it is clear that if evolution followed the Darwinian plan, it must already have travelled far, though we find no evidence whatever of any intermediate stages upon the way.

CHAPTER IV

THE HOLLOW CURVE

THE chief result of the work upon Age and Area, perhaps, was the discovery of the "hollow curve of distribution" (cf. chap. xviii of *Age and Area*, p. 195), a curve which shows in all cases of distribution that I have yet examined, whether of animate or even of inanimate things. My opponents have gone to great trouble to show that it holds, for example, with the names in a telephone book, or even with the distribution by size and shape of a pile of gravel, in other words that distribution is in general what one may call very largely accidental, and not determined by adaptation in so far as concerns general distribution about the world, which is exactly what I wished to prove.

The curve was first noticed in 1912 in regard to the flora of Ceylon, which consisted of 573/1 (573 genera each with one species in Ceylon), 176/2, 85/3, 49/4, 36/5, 20/6 and so on. If one take the first few numbers, one finds that the numbers to right and left of any single number (e.g. of 176/2) add up to more than twice as many ($573/1 + 85/3 = 658$) as itself, so that the curve must be hollow as shown in the figures below. It turns the corner between 3 and 5, and as the numbers get small it becomes more or less irregular.

The curve was also found to show, but not in such detail, with the areas covered by species. If one divide the species of a genus or family into those of large, small, and medium areas, one finds that if one add together the numbers in the large and the small, they make more than twice as many as those in the medium, or in other words they make a hollow curve, like those shown in the illustrations.

Now not only does this hollow curve show with the distribution of species by areas, but it also shows with the distribution of genera in a family by the number of species that they contain. We must always remember that statistics must only be applied to numbers and to related forms, which as a general rule will behave in much the same way. Take, for example, the family Monimiaceae, of 88 genera and 887 species. The two largest genera, *Siparuna* with 107, and *Mollinedia* with 75 species, range

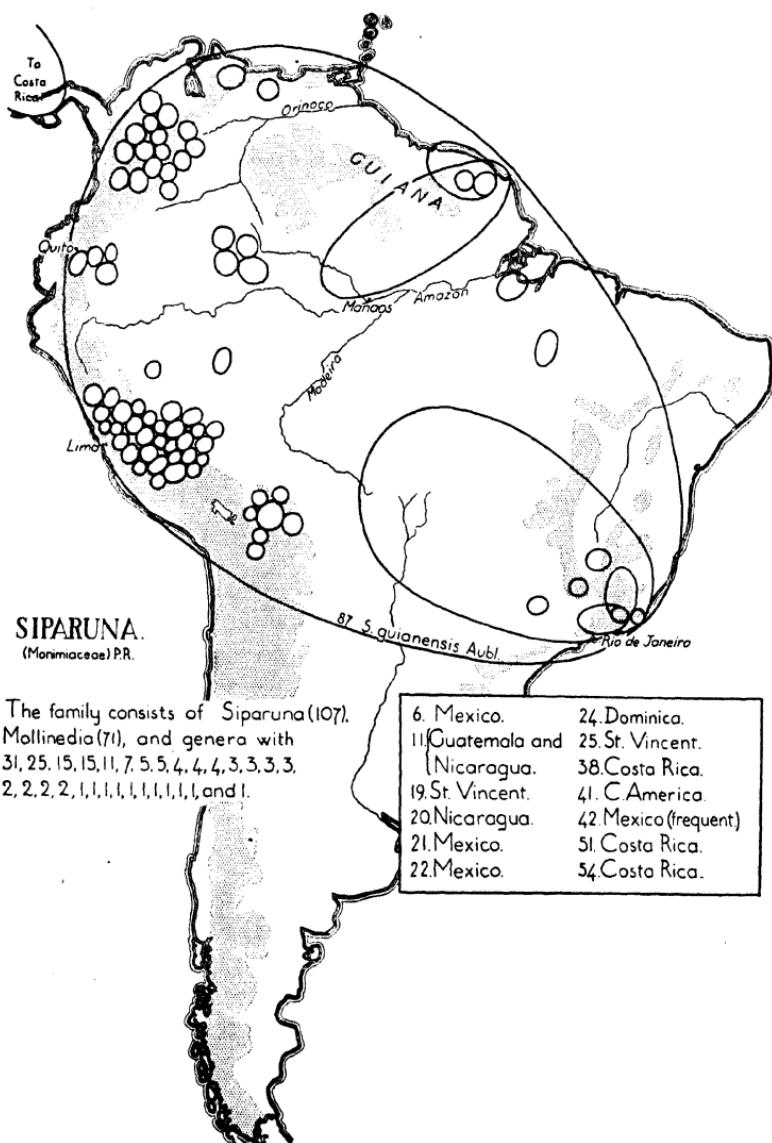


Fig. 1. Distribution of Siparuna in South America. The local species in the Andes etc. are simply massed together, not shown each in its own place. The numbered list shows the localities of northern species.

from Mexico to Rio de Janeiro or south of it, the smaller genera over less districts. *Siparuna* has one species that covers the whole South American area of the genus, some of intermediate areas, and a great many of very small areas. *Mollinedia*, on the other hand, though its total area is much the same, has only one species that even ranges as far as from Rio de Janeiro to Monte Video; most of its species are quite local, and over 95 per cent are so local as to count as relics under the natural selection conceptions. Is it a failure because of the small areas occupied by the individual species, or a success because of their number, and the area occupied by the genus as a whole? What is selection doing in these two cases? And still more, what is it doing or going to do with the rest of the family, where the genera contain 30, 25, 15, 15, 11, 7, 6, 5, 4, 4, 4, 3, 3, 3, 2, 2, 2, 2, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1 species respectively? One cannot draw a line in a curve like this, to separate the sheep from the goats. Relics would not be made in steadily diminishing numbers, nor would local adaptation be neatly graduated like this. All families of reasonable size show the same curve, as seen in fig. 2, which gives the fifteen largest families of flowering plants. Close together though they are, the curves never touch. When turned into logarithmic curves, as in the next figures (3, 4), they all give approximations to straight lines, i.e. they have the same mathematical form, and must be the expression of some definite law which is behind evolution and distribution, and does not agree with current views about these subjects. Many distributional subjects show the same form of curve, as may be seen in fig. 5, which shows families of plants and animals, lists of endemics, floras, fossils, and areas occupied, all mixed up. The curve shows in the names in the telephone book, where the very common names are few, the very uncommon many. It shows in the list of numbers of hotels in towns in the advertisements in *Bradshaw*, where (in the one examined) only London and Bournemouth had large numbers, while a great many had only one each, and there were a few in the intermediate numbers.

This similarity interested me very much, and I have lately completed a study of the distribution in Canton Vaud (Switzerland), where I live, of the surnames of farmers, a class who move about less than others. Vaud is about the size of Gloucestershire, but divided into valleys often separated by very high mountains, which make intercourse between the valleys difficult. After a day on the farm, a young man is not going to cross a high moun-

tain range to see his best girl, but marries in his own valley. The result has been a very interesting distribution of surnames.

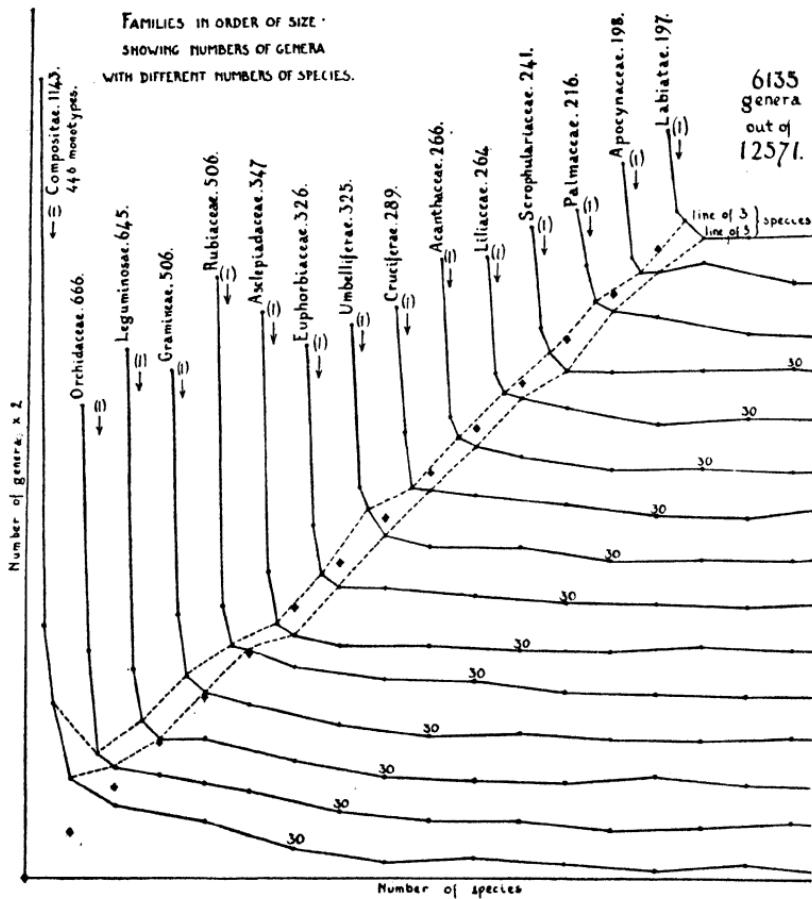


Fig. 2. Hollow curves exhibited by the grouping into sizes of the genera in the first 15 largest families of flowering plants. Each curve is diagonally above the preceding one, as indicated by the heavy black dots (points of origin). Note that the curve almost always turns the corner between the point marking the number of genera with 3 species, and that marking the number with 5 (indicated by the dotted lines). The number after the name of the family shows the number of genera in it.

In a great proportion of the villages in the canton, some hundreds in number, there are local names found only (i.e. endemic) in one village each, sometimes on one farm only, sometimes on two or more. Sometimes the names occur in two or

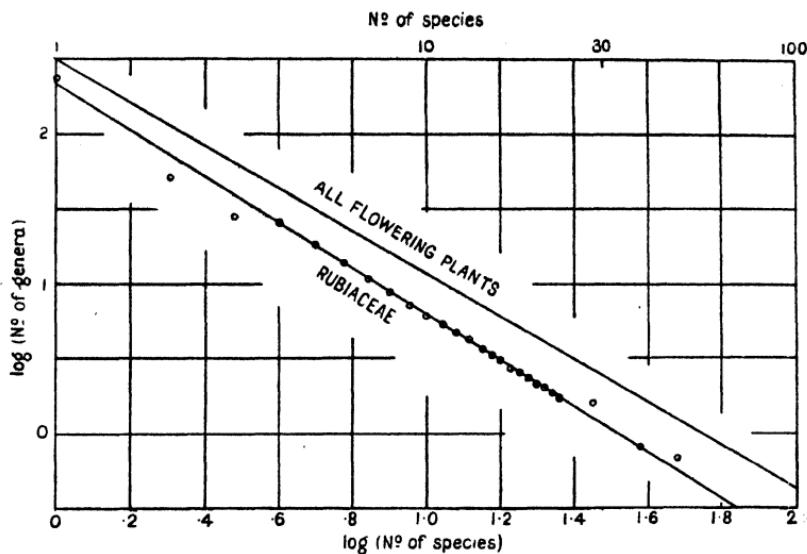


Fig. 3. Logarithm curve for Rubiaceae (from Willis, *Dictionary*).

(By courtesy of the Editor of *Nature*.)

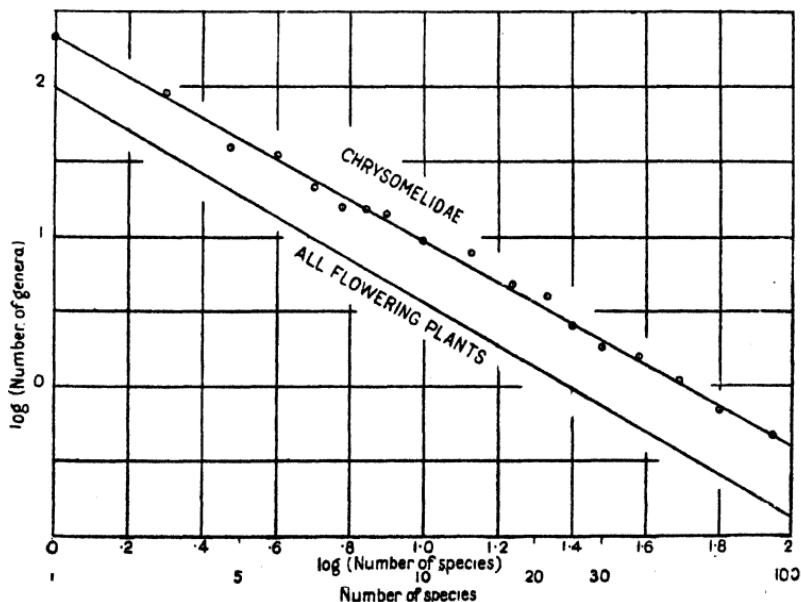


Fig. 4. Logarithm curve for Chrysomelid beetles (from old Catalogue).

(By courtesy of the Editor of *Nature*.)

more villages, but always in diminishing numbers as one goes upwards, just as with the plants. Most often the villages are in the same neighbourhood, but at times they are as far off as a

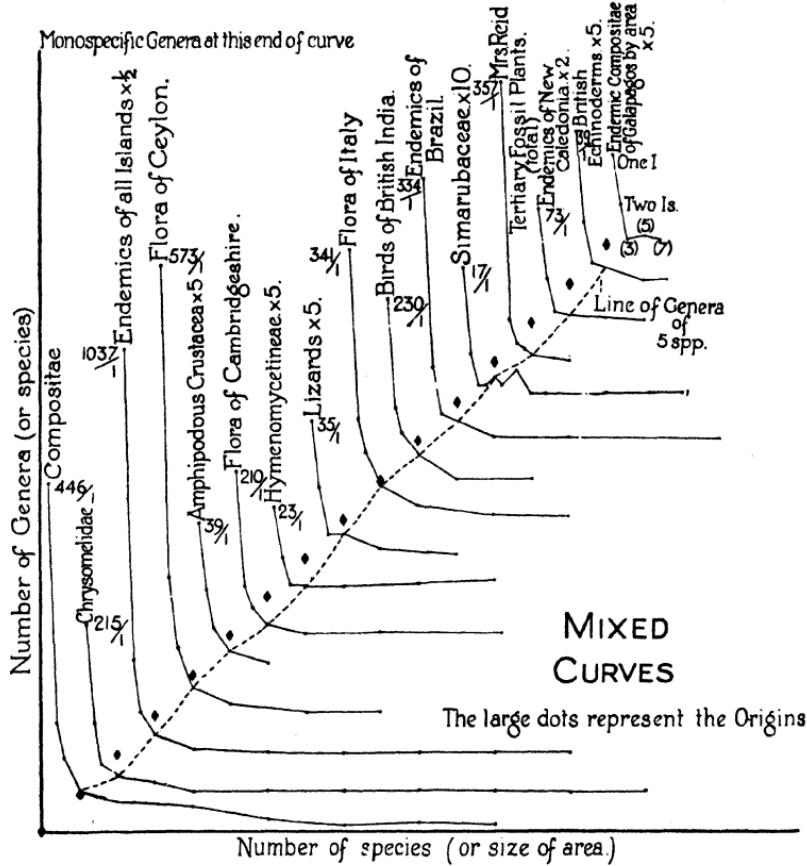


Fig. 5. Mixed curves, to show the close agreement of the hollow curves, whether derived from families of plants grouped by sizes of genera (Compositae, Hymenomycetinae, Simarubaceae), families of animals (Chrysomelidae, Amphipodous Crustacea, Lizards), endemic genera grouped by sizes (Islands, Brazil, New Caledonia), local floras grouped by (local) sizes of genera (Ceylon, Cambridgeshire, Italy), local faunas (Birds of British India, British Echinoderms), Tertiary fossils by sizes of genera, or Endemic Compositae of the Galapagos by area. [By courtesy of the Editor of *Nature*.]

man can walk in one or two days, their distances and the tracks on which they lie showing the directions of emigration of young fellows in search of work.

The distribution of species of plants that occurred in Ceylon,

for example, *outside* the island, was found to go, on the average, with their distribution inside the island,¹ but natural selection could not adapt a plant that was to come, say from West Africa, to suit Ceylon better than a plant that had only come, say from Bombay. If anything, one would expect the latter to suit Ceylon the better. And the same thing showed with the names of the farmers. Rochat is a very common name in the valley of Joux, and has spread farthest into the country round, while the names that are less common have spread less. It is impossible to maintain that the possession of the name Rochat gives any advantage in the struggle for existence as against the name Capt, which is less common in Joux, and has not spread so far beyond it (fig. 6). Natural selection can have nothing to do with the distribution of surnames, which behave just like species of plants.

All these various curves match, and must be determined by the same rules. There would seem to be a necessity to reconsider the idea that distribution is determined by natural selection, as indeed we have already seen. Adaptation can only be to the conditions that exist round about the plant, and it is absurd to suppose that the bulrush or the silverweed, for example, that (in the same specific form) occurs in New Zealand as well as in Europe could have become, in Europe let us say, adapted to New Zealand conditions. That it suits them is simply due to luck, and to local adaptation, as it slowly moved from place to place. But in any place where it was not fairly well suited, it would usually be killed out remorselessly and promptly by natural selection.

Many other cases might be brought up, but the fact that distribution shows these hollow curves, which cannot be explained by aid of the theory of natural selection, will suffice to show that that theory in its turn is meeting with almost insuperable difficulties. It was difficulties like this which made my friend Dr Guppy, who had devoted most of his life to the study of distribution, adopt in 1906 the theory of evolution by differentiation, whilst, as the result of completely independent investigations upon different lines, I myself adopted it in 1907. The theory itself is pre-Darwinian. The idea that underlies it, as formulated by Guppy, is that in the early days of the flowering plants the climates of the world were damper and more uniform. The world as a whole seems to have become drier since that time, so that the

¹ I.e. a plant widely distributed *in* Ceylon was on the average widely distributed *outside* it.

climates must have become more differentiated into damper and drier, warmer and colder, etc., than they once were. With them the plants have become differentiated, and it was commonly supposed that this was done, as in the theory of natural selection,

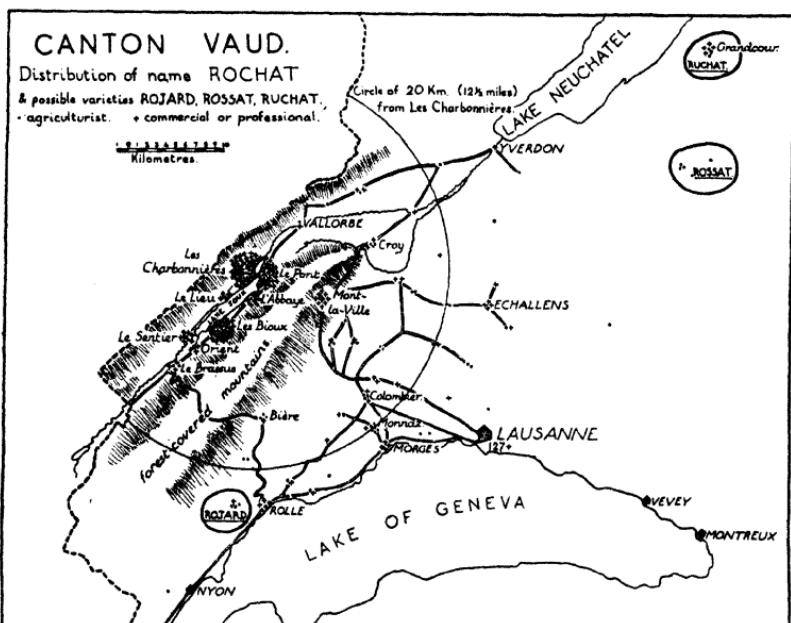
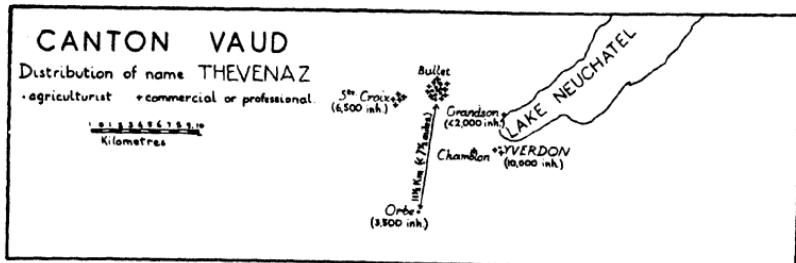


Fig. 6. Distribution of two surnames, Thevenaz and Rochat, in French Switzerland.

more or less in suitability to the various climates, but that the whole specific or other difference appeared, not by gradual adaptation, but at one step. The writer, however, is not prepared to admit that these things are *necessarily* connected, without further evidence.

To this, I have added the facts of the hollow curves, which are universal, not only in the distribution of plants and animals, but in other things, as we have just seen in the case of that of the farmers' surnames in Vaud, which matches to a nicety the distribution of plants. It seems to me impossible to reconcile these curves with the theory of natural selection, and there are other very serious objections to this latter theory. To reconcile the theory of differentiation with the hollow curves, I have added to it the supposition that the evolution that goes on, and which is shown in the morphological characters of plants, has little or nothing to do, directly, with adaptation, and certainly not with direct adaptation. The characters do not necessarily indicate adaptation at all. Every now and then a character appears, like, for example, climbing habit, of which natural selection can make use, and which is therefore retained, but natural selection was not the direct cause of its (complete) appearance, nor was its appearance, in all probability, as accidental as that theory would involve. It appeared full-fledged, and was advantageous, or at any rate not harmful. And if it had no necessary adaptational value behind it, there was no particular reason why a species showing it should spread at a different speed from other species of the same or closely allied genera, a supposition which at once made the hollow curves a normal feature of distribution. And there was also no reason why the many new species that have appeared should not appear at a rate that was in any case not determined by the necessities of adaptation, as we have seen in the case of the Podostemaceae. A species that reached a sand dune, for example, if it were reasonably suited to it upon arrival, would gradually adapt itself in more detail to some definite local conditions there, by physiological adaptation controlled by natural selection.

What the mechanism was by which this evolution was carried on, we do not know. I suggested in 1907 that "a group of allied species represents so many more or less stable positions of equilibrium in cell division".

The occurrence of the hollow curve for distribution of plants by areas, or for distribution of genera by numbers of species, shows that neither in geographical distribution (strictly so-called) nor in evolution can natural selection be invoked as it once was, as the principal factor. Any influence that it has must either be very small, or else exerted in an indirect way. One cannot, upon such a curve, draw any dividing line, and say that those upon

one side are to be regarded as successes, those upon the other as failures. Nor can one picture to oneself a system in which the number of failures that die out (and in all families more or less alike) is at first to be about 38 per cent (the monotypic genera, of one species), then only about 12 per cent (the genera of two species) and so on in decreasing numbers.

CHAPTER V

CONTACTS WITH DARWINISM, *continued.* MUTATION

THE coming of mutation was mentioned above (p. 14) and it was pointed out that it seemed to get over some, at any rate, of the difficulties inherent in the employment of gradual variation. In particular, as the new form was qualitatively, and not merely quantitatively different from the old, the change was differentiating. Further, it was practically irreversible, and might also be hereditary.

But it was gradually realised that its employment brought in its train other difficulties which were almost as great, so long, at any rate, as one adhered to natural selection as the driving force in evolution. This adhesion definitely handicapped the theory, preventing it from giving its proper stimulus to biological progress. Since people wished to combine it with natural selection, they had to stipulate that mutations must be very small. It was very hard to see how it could work with large mutations that might effect such differences as distinguish the Monocotyledons from the Dicotyledons, or even those that divide one family or genus from another, and which might change the whole character of the plant. If these were to be allowed, one could no longer imagine progress by small, gradual, and progressive adaptation, and this, determined in every detail by natural selection, was still the ruling principle invoked in evolution. If we remove direct advantage from the list of factors that may be immediately operative in causing evolution to go on, it is evident that the structural mutations that distinguish one form from another need not, perhaps even cannot, proceed in gradual stages, unless there be, as of course is by no means impossible, some at present inscrutable law that guides them. But fossil evidence gives but little support to this conception. Real intermediates are rare; what are commonly called intermediates are usually things that combine some of the characters of one with some of the other. If one find a plant showing, to give an imaginary case, four of the characters of Ranunculaceae to three of the Berberidaceae, it is sure to give rise to discussion and dispute.

More than thirty years ago the writer published a paper upon the distribution of the Dilleniaceae (72), in which he adopted the notion that mutation might at times be so large that there might appear in one step a new species, or perhaps even a new genus. Intermediate stages were not considered to be necessary, though it was pointed out that in one or two cases intermediate forms, perhaps hybrids, were found living side by side.

By that time the author had completely discarded the theory of natural selection as the chief driving force in evolution, regarding it primarily as a means of getting rid, promptly, of anything that was seriously unsuited to the conditions under which it had to live. There was, of course, no definite reason why selection should not at times, under favourable circumstances, produce new forms, but it seemed unlikely that such production was at all common, or that it should produce forms of specific rank. It could not be looked upon as operative in regard to the bulk of the morphological characters which show us that evolution has gone on, and which in consequence have always tended to be regarded as in some way showing progressive adaptation. The author had also abandoned the idea that there was such wonderful *morphological* or structural adaptation in the flowering plants. Each, of course, must be fairly well suited to the place in which it grew, for if it were not, natural selection would soon dispose of it; but that was all, in most cases. Real adaptation was largely internal as was clearly indicated (1) by the enormous range of many species without any serious morphological change from one region, or one set of conditions, to another; (2) by the great numbers of plants that were to be found in the same conditions (as nearly as made but little difference) and yet showed such great morphological differences that they could be classified into many different families and genera, though they might all come into one ecological category, like the Podostemaceae or the plants of a moor or a sand dune. The common plants of a moor in Britain, for example, include *Betula*, *Calluna*, *Carex*, *Cornus*, *Empetrum*, *Erica*, *Kobresia*, *Listera*, *Molinia*, *Nardus*, *Potentilla*, *Scirpus*, and *Vaccinium*, covering a great range of the flowering plants, as can be seen at a glance. Another indication (3) was the great numbers of species of one genus that might at times be found in similar conditions, like *Mesembryanthemums* in South Africa, while single species of other genera ranged over great differences in conditions.

The structural differences that showed in plants to such an

extent were often so clear cut, and so distinct, that it seemed to the writer quite evident that they must in general have been formed by sudden change, or mutation. Gradual change, picking out advantageous variation, would be very unlikely indeed always to produce *the same structural character*, such, for example, as is shown by a berry or a drupe, or by opposite leaves. Why should berries be most often found in the near (systematic) neighbourhood of capsules, drupes in that of achenes or nuts? Why should selection pick out leaves that were *exactly* opposite, ovules with the raphe exactly dorsal or ventral, or why such clearly marked and exactly formed fruits as capsules, berries, etc.? Selection would obviously act with decreasing force as the leaves came nearer and nearer to being opposite (or alternate, for then they show a definite phyllotaxy or arrangement), or the raphe to being dorsal or ventral, etc. In actual fact, between many of these characters, intermediate stages were not possible. One could only take the one or the other side of a very divergent variation, such as alternate *or* opposite leaves, dorsal *or* ventral raphe, etc. The mutation, in so far as the characters themselves were concerned, paid no attention to functional or adaptational requirements. It was impossible to conceive of any adaptational need that would ensure that all Monocotyledons should have a single cotyledon, together with a parallel-veined leaf, a trimerous flower, and a peculiar anatomy. There is not even a "monocotyledonous" mode of life to which this great morphological change might be supposed to adapt them. For that matter, there is not even a "ranunculaceous" or a "thalictroid" mode of life. The larger a genus, family, or other group of plants is, the greater is the variety in the conditions of life in which it is found (comparing, as usual, only related forms), and also the larger the area covered by single individual species of the family or genus.

To return to the Dilleniaceae; assuming that mutations could be of generic size, the author drew up a scheme according to which the whole tree of the family could be looked upon as derived by descent from a genus so comparatively simple in structure, and so widely distributed, as *Tetracera*. A sketch was drawn of a suggested manner in which the evolution might have proceeded, showing all the existing genera, which might even be the whole tree of the family. Of course some geological or other catastrophe might have killed out some more or less local genera, though it would be unlikely to have done so to any genus that was already very widespread. Incidentally *Tetracera* is not the

largest genus in the family, but it is the most widespread, and when these two characters do not agree in pointing out what is probably the oldest genus, the author considers that distribution rather than size should be regarded as more important.

In thus supposing that a genus could appear at one stroke, and that one genus could, directly, give rise to another, the author was definitely going beyond mutation pure and simple, and adopting the theory of differentiation, in which, as the changes were large, the idea that the morphological differences represented adaptational improvements was discarded. In other words, though evolution was unquestionably going on, and was on the whole, though more notably in the animal world, producing higher and higher types, there was no need to suppose that there was necessarily any adaptational reason in the innumerable structural changes that showed themselves in the course of that evolution, and indeed showed that evolution was going on at all. It seemed much more probable that most of those features which we were accustomed to call adaptational improvements had appeared already full-fledged. If new features that thus appeared were really harmful, or met with ill-luck, they were promptly removed by the action of natural selection. If they were beneficial, or not harmful, and met with average luck, they were retained.

The sketch showed the way in which it was suggested that evolution had proceeded, from the large and widespread genera down to the small and local, but there was then about as much chance to prove this kind of mutation as to prove that natural selection could do what was required to form a new species, for it must not be forgotten that this has not yet been done. There is some reason to suppose that it can produce new varieties, but no proof that it can cross the line of mutual sterility that usually lies between species. Both theories derive varieties from a parent species, but selection derives them from a parent which is at an earlier stage of development, and perhaps fated to die out, the varieties being considered as on the way to species. Differentiation does not admit this, but regards them as later stages of development by mutation than the species that gave rise to them, and with which they are not necessarily in competition, though perhaps they may sometimes go on, by further mutation, to become new species. The essential point at present, for differentiation, is to prove that evolution proceeded in the direction from family to species, and not the reverse.

When one looks at the great differences that exist, for example, between the Dicotyledons and the Monocotyledons, and these in several different points, it seems to be an unnecessary handicap to accept the idea that mutations must necessarily be small, especially when we have no facts to prove that this must be the case. The characters are so completely unrelated to anything in the way of adaptation that it becomes very difficult to conceive of them as having been gradually acquired, especially when one remembers that intermediates between them are all but impossible, and could not in any case have any adaptational value, so that unless there is some recondite law in the background that can force things to proceed in such a manner, there seems no reason for it. There might for example, be (probably is) some physical or chemical law that at present we do not know, compelling genes or chromosomes to behave in a certain way.¹ But as one sees the phenomena at present, how can one pass by gradual stages from two cotyledons to one (or vice versa), from net veining to parallel, from a 5-merous to a 3-merous flower, from the one kind of anatomy to the other? The only reasonable way to account for it is to suppose that the characters of Mono- and Dicotyledons were handed down as the lines of descent resulting from a mutation in very early times which split off the one from the other. No adaptational difference can be found, nor is there any "monocotyledonous" mode of life. As one comes up the scale from species, the plants are found to grow in greater and greater variety of conditions, and to belong to more and more of the various ecological groups. If monocotism suit a grass or a bamboo better than dicotism, why does it also suit a tulip, a *Zostera*, a *Potamogeton*, an iris, or an orchid? And why, if there is any adaptational difference between the two great groups, do they occur with such regularity in almost every part of the world in the proportion of one to four? There are small places where these figures vary very much, but the only large ones are usually near the limits of vegetation, a fact which suggests that there are differences in age between the two groups. Hooker pointed out this numerical relationship in 1888 (18), and it remains one of the many problems in geographical distribution which are completely inexplicable upon the hypothesis of natural selection, and which are left unmentioned by its supporters.

Another direction in which the theory of mutation makes

¹ My friend Dr C. Balfour Stewart suggests that it is probably electrical, as is probably the splitting of the chromosomes in reproduction.

things much easier to understand is the widespread correlation of characters, for which natural selection can offer no explanation. Why is the possession of tendrils, or of hooked leaves or stems, always accompanied by a weak and flexible stem? Why has a dorsiventral leaf, such as is possessed by a vast number of plants, always a layer of palisade tissue towards the upper side, for making the best use of the light that falls upon it? Why, in the Compositae, have the heads of flowers an involucre of bracts, why has the style two stigmas, why is the ovary unilocular, why is there only one ovule and that erect, and why is there no endosperm? And why do all these characters go together in practically every instance in a family of 18,000 species? The same sort of questions may be asked for any other family, whilst they would be absurd in the case of adaptational characters. Nothing but descent from a common ancestor (or ancestors) will explain them, and evolution upwards from individuals and varieties will not do it; it must have been the other way, as differentiation would have it. Evolution apparently must go on, at any rate if the appropriate stimuli are present, but there is no necessary adaptational reason for much of it, at any rate, and we find practically no gradual stages in the fossil record. To accept mutation, and that of any necessary size, would seem to be the simplest theory upon which to work until something better turn up.

An objection often brought up is that no such mutations—large, viable, not recessive, and not lethal—have been seen. But no one has ever seen a species formed by natural selection. Yule has estimated that one such mutation in fifteen to thirty years, upon any small spot of the earth's surface, would be sufficient to account for all the flowering plants that exist. The chance of seeing such a mutation is all but non-existent, and if the result were found at present, people would at once put it down as another relic and leave it at that. Until we can control mutation—and signs are not wanting that we may be able to do so at some future time—we can hardly hope to get proof for this proposition.

One must not forget that the mutations that have been studied have, as a rule, been mutations that have occurred in cultivated plants, or otherwise in unnatural conditions, conditions which in themselves perhaps stimulated a greater mutability than usual. We have not properly considered the case of mutations under completely natural conditions, which are well known to be much less common. If a mutation appear in a seedling of some tree in

the jungle, the chances are that it will inherit the suitability of its parents to the local conditions, and that if the mutation be not seriously harmful, it will not be interfered with in any way by natural selection, and will be allowed to survive, and in time, if hereditary, to propagate itself. May it not be that something of this kind is an explanation of the great majority of the innumerable structural differences that we see in plants, and which so often only appear when the serious struggle for existence is over, or practically over? One cannot imagine that it can have any importance in the struggle for existence whether a plant have or have not one or two cotyledons, a parallel-veined or a net-veined leaf, a 3-merous or a 5-merous flower, and so on. To the vast majority of the characters upon which we base our classifications natural selection is probably completely indifferent. It is well known, incidentally, that most of those characters which we consider as usually of family rank (App. I) may at times appear as generic, or even specific, so that it is evidently quite easy for them to be acquired, while at the same time the structural agreement between them is amazing. Nothing but sudden mutation will easily account for such phenomena.

A case in which mutation of this kind looks as it might have happened in nature is that of the columbine (*Aquilegia*), which looks as if it might have arisen from the larkspur (*Delphinium*), the latter having a dorsiventral flower with one spur, the former a regular flower with five spurs. Nothing but mutation can cross the (numerical) gap between these genera, and one actually sees an almost exactly similar mutation happening frequently in the toad-flax.

A good illustration (and dozens similar to this could be given) of the very great probability of large mutation is that afforded by the three families Centrolepidaceae, Eriocaulaceae, and Restionaceae, all of which, independently, split into two sections, Diplantherae with dithecos anthers, and Haplantherae with monothecous. One cannot conceive of this by anything but a direct mutation, which would produce morphological similarity in all.

Some quotations bearing upon this subject may be made from a paper now of some age (57), in which attempts were made to show that local or endemic species were usually separated from the widely distributed, and usually fairly closely related, species that accompanied them by differences which could only be passed over by mutations, often "large".

Ranunculus sagittifolius, confined to the high mountain region about Nuwara Eliya (Ceylon), differs widely from the only other Ceylon buttercup, *R. Wallichianus* (South Indian also), which occurs side by side with it, though in drier and sunnier places, but is closely allied to *R. reniformis* of the mountains of the western Indian peninsula, differing mainly in the petals, which are five in the Ceylon species, twelve to fifteen in the Indian one. . . . Are we to suppose the conditions of life so different in the Ceylon and Indian mountains that a five-petalled flower will suit the one, a twelve-petalled the other? Or how is the one to pass into the other, or both to arise from a common ancestor, except by discontinuous variation? Can it be supposed that the simple obovate-lanceolate leaf of *Acotrema intermedium* fits it for the Kitulgala district (Ceylon), while the pinnate leaf with linear-lanceolate segments of *A. Thwaitesii* fits that species for the Dolosbage district, but a few miles away, a trifle higher up, and in a similar climate? . . . *A. lyratum*, characterised by very long peduncles, is found only on the summit of Nillowe kanda, an isolated precipitous rock. . . . is it to be supposed that the long peduncles are any advantage? . . . What advantage can the two ovules of *Polyalthia Moonii* and *P. persicifolia* be against the one of the other species? *P. rufescens*, another species with two ovules, and closely allied to both, occupies the Cochin district of South India, and why should there be three species in so similar a country? . . . And how did the one form arise from the other, or both arise from a common ancestor, except by mutation? Similar queries might be asked 800 times for the 800 endemics. . . . in the Ceylon flora.

The only possible explanation to my mind was that provided by the "parent and child" theory, that parent and child might, and very often did, exist side by side.

The general principle on which India and Ceylon have been peopled with the many species which they contain would seem to be that one very common species has spread widely, and, so to speak, shed local endemic species at different points, or in other cases that one species has spread, changing at almost every point into a local endemic species, which has again changed on reaching new localities.

A very good proof for mutation, and indeed for differentiation also, is provided by the work done by Mr G. Udny Yule and the writer upon the statistics of evolution (76). We showed that the evolution of new genera out of old followed with very great closeness the rule of compound interest. After some time one genus becomes two, and so on. But if genera are formed like this it is hard to believe that they can have been formed by gradual steps,

and it would also show that the larger must be in general the ancestors of the smaller. Evolution seems to have proceeded upon a definite plan; "the manner in which it has unfolded itself has been relatively little affected by the various vital and other factors, these only causing deviations this way and that from the dominant plan".

CHAPTER VI

CONTACTS WITH DARWINISM, *continued.* ADAPTATION

ADAPTATION, or suitableness, with an implied meaning of having been suited by some particular agency, is a subject that has been as much discussed as any in biology, and especially since the publication of the theory of natural selection, which is essentially based upon it. Under that theory a new organism only comes into existence because it is an adaptational improvement upon that from which it is derived. In other words, improvement in adaptation is the only reason for which new organisms are evolved. But the only thing that shows that they are new organisms is a structural or morphological difference between them and other forms, even if the latter be obviously closely related to them. It was, therefore, taken for granted (it could hardly be otherwise) that *the morphological or structural characters were the expression of the adaptation that had gone on, and therefore had, themselves, a greater or less adaptational value.*

Once this was fully realised, there was a great rush into the study of adaptation, especially during the 'eighties and early 'nineties of last century. But in spite of all the work that was put into it, no one ever succeeded in showing that even a small percentage of the structural characters, that were the reason why plants were divided into so many families, genera and species, had any adaptational meaning or value whatever. No value could be attributed to opposite as against alternate leaves (or vice versa), to dorsal against ventral raphe, to opening of anthers by pores or by slits, and so on.

In the characters of the plants of average moist climates (often called mesophytes, as occupying the middle position), it was very difficult to find anything that could be called in any way adaptive, except those general characters which are common to most of the higher plants and occur in almost every kind of conditions, such as roots (which are adapted to taking up food), leaves (adapted to forming food by aid of the energy of light taken in), flowers, fruits, seeds, etc. But as one went outwards to either extreme, to the water plants (hydrophytes) on the one side, or to

the plants growing in dry climates (xerophytes) on the other, one began to find characters more or less individual to the species, that had something definite to do with the mode of life of the plants, and which therefore might be called adaptive characters. On the one side one found the somewhat negative characters of absence of strengthening tissue and absence of stomata, with diminution or absence of the roots; on the other side one found the more positive characters such as sinking of the stomata in pits, hairy or waxy leaves, and in the most extreme cases, such as the cacti, of storage of water in the tissues. But few of all these characters, of whichever group, though they might make great changes in the general look of the plants, were of great importance in the separation of plants into species, or into genera, and still less into families. There is little evidence that even such great adaptations as are involved in the development of hydrophytes or of xerophytes can cause such great morphological or structural differences as actually exist between plants. A mere glance at the composition of any ecological group of plants that are suited to any given situation is sufficient to show the truth of this. Take, for example, the plants that occur in boggy places in Britain, of which lists may be found in Tansley (44) or Bonnier. There are about twenty genera represented, of which eight are Monocotyledons, whereas the average proportion of Monocotyledons is only one in five. Among woodland plants they are one in three, whereas upon cliffs they are absent. Though the differences between them and the Dicotyledons are about the most important structural differences that occur, there is no evidence to show that they have any adaptational value whatever. The bog plants also show both alternate and opposite leaves, superior and inferior ovaries, capsules that are septicidal and loculicidal, and that open by lids, that are divided into several loculi or have only one, whilst there are also achenes, follicles, berries, drupes, and schizocarps among the fruits. The twelve genera of Dicotyledons belong to ten different families, including both Polypetalae and Sympetalae, and so on. In Ericaceae, where two genera occur, one has a berry, the other a capsule. Nowhere is there any indication that the supposed structural adaptation had anything to do with the fact that they all live in bogs, and must therefore be adapted, or suited at any rate, to that mode of life. Other British ecological groups of plants—those of chalk-downs, mountains, and dunes, etc.—will show similar results. Everywhere one finds that there are plants showing the important characters of

classification and distinction, and even showing, in many cases, both members of the contrasting pairs that are given in the list of family characters (Appendix I). These characters show no relation whatever to any of the ecological features that may give the character to the locality. Almost any family or genus, *if large* (i.e. old, upon the theory of Age and Area, with its subsidiary Size and Space) may be found in almost any kind of locality, represented by some of its species. For example, in the bog flora just mentioned, there occurs *Sedum villosum*, a member of a large genus of 450 species usually xerophytic. And not only so, but it is a hairy species, bearing a character usually specially associated with xerophytism. Morphologists have long maintained that structural characters have nothing to do, directly, with the life or functions of the plant, and it would appear that they are right in this contention, which violently contradicts the supposition of selection as a chief cause in evolution. The evolution that has produced more than 12,000 genera and 180,000 species has not been, primarily, an adaptational evolution, as the writer tried to show twenty-five years ago in the case of the Podostemaceae.

The agency by which plants were to become adapted to the conditions in which they were found was, of course, that of natural selection, for the competition upon which it is based, which we call the struggle for existence, will evidently kill out those that are in any way seriously unsuited to the conditions. It may also kill out some or many of those that are well suited, if they be in any way handicapped, as by too shady a position when in the seedling stage, by a poor water supply, or by many other things. But in itself this killing out would not produce any advance in complexity of structure or function, the things that we regard as showing that evolution has gone on. Certain assumptions were therefore needed. Only advantageous changes could be picked out, and it was therefore supposed that (usually) when a gradual change of local conditions began, some of the offspring varied in such a direction as to give them an advantage. It had also to be assumed that the parent did not vary in this way. The process being repeated in every generation (another assumption), the improved forms always winning, the difference from the parent ultimately became specific, showing as a rule more or less sterility when crossed with the parent. The parent was supposed not to adapt itself (yet another assumption), but to become a relic and gradually to die out for want of offspring viable in the new conditions.

For such a process to be successful, there are other assumptions that we must make. We have (1) to assume—which goes against much or most of the evidence—that a morphological change has some adaptational value, (2) that such a variation will appear at the time when it is wanted (for otherwise there will be nothing for natural selection to work upon), (3) that the conditions will continue to vary in the same direction long enough to permit of the adding up of small variations until the specific (sterility) line is passed, (4) that the operation is so strenuous that at some point upon the way the sterility line will be safely passed, (5) that at some point when the species is fully embarked upon the change, a better variation, but working in another direction, is not offered to it by nature, thus confusing the result, (6) that when one variation has achieved its full result, it shall be followed by another, often in a completely different direction (for one species usually differs from another in several characters) without interfering with the mutual sterility, and (7) that the variation is so eminently desirable that it will be followed up until the new structural feature, for instance alternate (or opposite) leaves, palmate, pinnate, peltate, stipulate or exstipulate, gland dotted, or other type of leaf, anther opening by slits, valves, or pores, dorsal or ventral raphe, achene, follicle, pod, nut, schizocarp, berry, drupe, etc., is *fully* perfected.

The whole thing is largely based upon the third assumption given above. For example, the climate (not the weather) must change gradually in the direction of warmer or cooler, wetter or drier. But these changes are well known to be so slow that they can only be detected in averages of a century or more—a period longer than the life of most plants, except many trees—whilst weather is continually changeable. Suppose a plant to have begun to vary in the direction of suitability to increased drought, and then there comes, as so commonly happens, a cycle of wetter years; what is going to happen then? Botanists have somewhat neglected weather effects, when compared with agriculturists. In the *Report of the Sudan Agricultural Research Service* for 1937, which I have lately reviewed, it is stated that the average good yields of the whole Gezira, in which the weather conditions were as stated, were reflected on the Government Farm, where the yields were much the same; “and once again we get an illustration of the comparatively small effects which local conditions may have”. This is familiar to all who have to do with crops, and puts considerable difficulty in the way of anyone who imagines

local adaptation to local needs, except upon very large areas. Would adaptation be likely steadily to follow a line based only upon averages, in such circumstances? It would hardly seem likely.

U 4 cotton, one of the great successes of cotton breeding, was locally bred at Barberton in the Transvaal for certain needs, and has proved to be a superior cotton for an immense area. But a Darwinian species would almost certainly be a species produced upon a local area, and if it began to spread about in its early stages it would be lost (as Fleeming Jenkin showed) by crossing with its neighbours, a fate from which U 4 was, of course, carefully protected.

Conditions other than those of climate or soil are hardly likely to change continuously in one direction, except upon broad general lines, such as a change from forest to grassland or vice versa, and even this is probably determined by climatic change.

There is another type of adaptation, which we may call adaptation to movable conditions. A climbing plant will remain adapted to climbing almost anywhere that there are erect plants, so long as it is suited to the climate and other general conditions. A water plant can travel over an immense area, finding suitable conditions in innumerable places. The American pitcher plant, *Sarracenia*, is now quite happily established in a bog near to Montreux, and so on.

Geographical distribution was also explained by the selectionists as based upon adaptation. The better adapted species were those that spread the furthest. But how did a species become adapted, let us say in Asia Minor, to the conditions that occur in New Zealand? It must be just a case of luck. If the species were old, so that it had plenty of time to adapt itself wherever necessary, and as in this case it would probably have a good deal of capacity to withstand extremes, or adaptability, it would probably be able to find places whose existence would enable it to get across the vast distances. When at last it reached New Zealand it would probably soon find places in which the conditions were sufficiently like those just left to enable it to live there. One would, perhaps, expect those plants that were evolved in regions where there was great variety of conditions to be those most likely to spread widely; it may be so, but we have at present no evidence to go upon.

In dealing with the adaptation of a plant to changed conditions man always tends to be in too great a hurry. When Europeans first went to the tropics, they tried to acclimatise there the plants

of Europe, with no success except in the high mountains, where many herbaceous, but rarely arboreous, things have taken a hold upon ground from which the original plant associations had been removed. In the same way they tried to acclimatise in Europe tropical things like the dahlia or the potato, but even after the lapse of centuries these plants remain "half-hardy". In both these cases the change of conditions was too great to allow of physiological adaptation, which might perhaps have taken place in a gradual acclimatisation over a very long period of time with only very slight alteration in conditions at each step. Or it may have been only that the range of capacity to withstand conditions was not sufficient even after the utmost had been done in acclimatisation. Time and gradual progression are the most essential things in acclimatisation.

A very great difficulty in the path of acceptance of natural selection as a cause for gradual adaptation is the fact that so many of what look like real morphological adaptations require so much correlation. Climbing plants come into this group, though they are obviously well suited to climbing. The habit cannot be difficult to acquire, for there are so many cases of the closest relatives, one climbing, one erect. A climber also needs a support, which is usually an erect plant, so that erect plants must have been the earlier. But one cannot imagine natural selection picking out the beginnings of weak and flexible stems, whether by gradual change or by small mutations. And when at last they were formed, as obviously there would be no value in developing tendrils or other means of climbing until the stems were weak, they would collapse into the darker lower levels of vegetation, and would have to undergo physiological adaptation to living in greater darkness. Then they would have to learn to form climbing organs, and finally, learning to climb, they would once more have to adapt themselves to life in greater light. And what use would the beginnings of tendrils or other climbing organs be? And why, after having learnt to live in greater darkness, should the plant want to grow up into the light once more? Yet it would be dragged up by the tendrils, and would probably suffer from the excess of light. There is too much, and too complicated internal adaptation required, to say nothing of the external. One must look with great suspicion upon such an easy interpretation of such structural features as climbing stems as being simply adaptations. If they were gradually formed, the work was too complicated for natural selection to perform.

It is clear that in adaptation to climbing a large part of the adaptation, if not perhaps all, must be internal and physiological, and we are inclined to think that it is to such adaptation that the name should be practically confined, while such things as climbing plants might be called *suited* to climbing. If a plant, as will usually be the case, move only a very small distance from the parent, it is probable that it will not need more than the minimum of physiological adaptation to suit it to the new place, and so on at every move. But such adaptation will not necessarily show any morphological changes visible to the outside. If one look at the distribution of such a widespread plant as *Hydrocotyle asiatica*, which ranges from the plains of Ceylon, with a temperature range of 70–90° F., to the south of New Zealand with winter snow and frost and a weak sun, one finds it to be essentially the same plant throughout. The Ceylon plants are suited to the Ceylon conditions, the New Zealand to those of New Zealand. But it is customary to speak of it as "adapted" to both. If it suits them both, it must be just a case of luck, with local adaptation going on as it has moved from one to another. One very much doubts, after considerable experience with acclimatisation, if seed from the plains of Ceylon would suit New Zealand without a lot of previous physiological adaptation, or vice versa.

Liberian coffee was gradually acclimatised to higher levels in Java by carrying seed a little higher at each generation. In Ceylon, when we tried to acclimatise the beautiful *Cyperus Papyrus* with European seed, we failed, but seed from India was a success.

The whole question of correlation of characters is an extremely difficult one when looked at from the point of view of natural selection. If large, it implies that most of the characters concerned have no bearing upon natural selection, and do not interfere with the results produced by the modification in the first character, thus further implying that the change in that is sufficient to carry the new species past the line of mutual sterility that will usually divide it from the old. The characters of climbing plants had some evident connection, for all were useful in climbing, but that does not apply to the characters that one finds correlated in an ordinary species, which have no apparent connection of any kind, nor anything to which one can attach any adaptational value. Their best explanation seems to be that they have gone together in the apparently purposeless and unaccountable way in which characters in mutations so often seem to go.

The mere fact that the prominent genera that occupy any kind of marked ecological standpoint, such as a bog, a saltmarsh, a mountain, a chalk-down, are usually the large and widespread genera, is enough to show that there was but little selection—they were the oldest and got there first, and being adaptable they became functionally modified to suit their new surroundings.

What has been said about gradual adaptation applies equally to the view at present rather in favour that mutations were small, and that selection presently resulted in another small step, and so on. But what is to ensure that a small step in one direction shall be followed by a second, or that conditions shall continue to change in such a way as to make it worth while for such a thing to occur?

The balance of probability would seem to be in favour of the appearance of structural characters by single mutations, and in that case it seems rather absurd to talk about adaptations in them. The adaptation is rather the internal and functional adaptation.

It would seem quite possible that climatic conditions all over the world have been gradually differentiating and becoming more varied as time has passed. On the whole, they have almost certainly become drier, though probably not in such places as many coastal regions. This would affect newly formed species by gradually restricting their freedom of movement, or even by forming impassable barriers. To move in a region of more or less uniform climate would probably require comparatively little of fresh adaptation to each new habitat, but if the climate were changing from one place to another, this adaptation would have to be greater, and would presumably need more time. This would in turn make the rate of travel slower, and it is quite possible that the change of climate might, so to speak, pass it upon the way, and erect a barrier some distance in front, the species reaching the limit of possible acclimatisation. This would seem to have happened in Ceylon, for example, where the island is rather sharply marked out into dry and wet zones. Comparatively few species are found on both sides of the divide, and really frequent in both zones. Many genera show a number of species in the wet zone with few in the dry, others the reverse, whilst of the genera that are confined to one zone, most occur in the wet.

It is clear that it is somewhat stretching a point to say that new genera, arising locally, as we have seen will in all probability be the case, are adapted to wide spread over the world. As only

rarely do the really large families show a single genus with the range of the whole family, a feature very common in small and frequent in medium-sized families, and as still more rarely does that genus in a large family show a species with the whole range of the genus, it is clear that any adaptation responsible for wide spread must be generic. What is much more probably the case, inasmuch as these widespread genera are admittedly of simple rather than of complex type, is that the parent of the genus still possesses great adaptability, or suitability to a considerable range of conditions. This will enable it to move far with less difficulty than usual, and as at the same time its structural evolution, which has probably little or no relation to adaptation, will be going on, it will give rise to more and more species. These will probably inherit their parent's general suitability to conditions, but it is quite probable that it may all the time be getting less (perhaps at each mutation), so that each new species may be liable to become more localised than its predecessor in regard to the total range possible to it, while at any given time it will of course be more local on account of its greater youth.

CHAPTER VII

ISOLATION

IN a paper on the floras of hill-tops in Ceylon, published in 1908 (57), the author drew attention to the great proportion of local endemics—one-eighth of the total number of endemic species—that were to be found upon one only, or upon more than one, of the mountain tops of the south-west of Ceylon. The principal massif (the central) is to the south-west, a smaller to the north-east of it, and there are a number of more or less isolated peaks separate from them, the most isolated being Riti-gala in the north of the island (p. 24). The highest summit, Pedurutalagala, attains 8296 ft.; Adam's Peak, the best known, is 7353 ft., and is rather isolated at the south-western edge of the central mass. There are ninety-seven well-marked Linnean species endemic upon these mountain tops, with eleven varieties of these or other species, some of which are usually reckoned as independent species. Of the species upon single mountain tops, there are no fewer than twelve upon Adam's Peak, which is so steep that its summit does not present any great area of vegetation for the last 2000 ft.

Since the widely distributed species, those that were not endemic to Ceylon, however localised in Ceylon they might be, were never confined to hill-tops, it was clear that there was, quite probably, some definite force or influence acting to cause these local endemics to exist in the places where they occurred. For a long time, opponents of my views maintained that they were relics of previous vegetation, and in fact this view is still popular. As they occur in general at higher levels than other species of their genera that are found in Ceylon, it was suggested that they had, so to speak, fled up the hills from their rivals. But if they could do this, they must have had a good capacity for internal, physiological adaptation, and it seems strange that they could not adapt themselves to staying where they were. And as most of the mountains rise from a central plateau, it seems very remarkable that so many of them should each be upon its own mountain. It seemed to me very probable that each was an endemic that had *arisen* upon the spot where it was found, and at various times, in conversation and elsewhere, I have suggested that the immediate

mechanism of their formation might be the action of cosmic rays, which would be more marked at high elevations.

It was clear that these mountain tops showed a distribution of plants like that which was shown by a group of islands forming an archipelago. Now the only thing obviously in common between the two was isolation, and I therefore drew the conclusion that isolation *as* isolation favoured the production of new forms. At that time we knew little or nothing about the genes and chromosomes, and since then Harland has put forward the likely suggestion that long continued gene separation may lead to gene change, which of course in its turn might lead to definite mutation. Since about three-quarters of this mountain-top flora has no special adaptation for distribution by wind or by animals, it is highly probable that individuals of the more widely distributed species lower down would very rarely reach the higher summits, whose plants would be, and remain, very isolated. In this connection it is worth special notice that the islands which show considerable local endemism, like the Hawaiian islands, are very commonly mountainous.

Whether the mutation which the author considers to have been the origin of any one of the species was due to one or the other cause, or to both, there would not be, in either case, any serious opening for gradual adaptation under the influence of natural selection. It must also be remembered that the number of individuals is very small (cf. p. 25). In this connection, I may quote from *Age and Area* the footnote on p. 206: "A few days before I left Rio, Dr Löfgren found, on a little island about three miles off the coast, a new and very distinct *Rhipsalis*, of enormous size. He told me that there were only four examples on the island." I may also refer to the examples given in the same book on p. 151.

Sixty-eight of the 108 endemics (including the eleven varieties) are found upon one mountain only, the other forty upon more than one. It is a very striking fact that these mountain endemics belong, not to small and local genera, but chiefly to large and widespread ones, as was shown on p. 26.

The general conclusion from this piece of work is that isolation favours the development of new forms, and that local conditions have but little effect in developing, though they may have much in determining the survival of, these new forms, and that consequently natural selection, upon adaptational grounds, is unlikely. It is more than doubtful whether any given species has been

specially adapted to the exact local conditions in which it is found, except by the internal, physiological adaptation that must always be going on. It would be killed out at birth if not reasonably well suited to the local conditions.

Turrill (47) has shown that in the Balkans one may find pairs of altitudinally differing species like *Bellis longifolia* and *svylvatica*, a fact which affords further evidence in favour of the author's view that isolation and elevation, one or both, may lead to the formation of endemic species upon mountains. In Ceylon, of the sixty-two genera represented by endemic species upon mountain tops, forty-three also have endemics at lower elevations, and only nineteen have not, a fact which makes the supposition that those of high levels are relictus seem a little far-fetched.

The Podostemaceae as a family are very isolated, and they grow submerged in water, usually at what are only moderate elevations, yet they have many species. Though isolated from other plants, they usually cover their own habitat, the rocks, fairly thickly, so that one hesitates to suggest that they would have so many species were they really isolated as individuals. It would seem more likely in their case that they owe their numbers to the overhead force of plagiotropism that is always at work upon them. There are probably quite a number of causes that may lead to the formation of new species.

Lakes formed by elevation of the coast of the Black Sea contain, I am assured, endemic species of cockles, a fact which would seem to favour isolation, especially as they are close to sea-level.

Siparuna (p. 35) has the great bulk of its local species in the mountains rather than in the plains, and the same is the case with many other genera, whilst many of the isolated islands that contain so many endemics are also mountainous. These facts might seem in favour of elevation (cosmic rays) rather than isolation, but other plants, such as the Dipterocarps, show many endemic species in the plains, usually in dense forest. Here species formation is probably connected with age.

Probably both isolation and elevation may be potent causes leading to well-marked development of new species. In the former case mutation is quite probably due to slow gene change, as Harland has suggested, but this would probably bring about sudden mutation by the adding up of strains until they became so strong as to cause some sudden kaleidoscopic change. In the latter case, if the cause of mutation be some effect of the bombardment of the genes by cosmic rays, one might expect the

mutation to be sudden, and as most of the mountain endemics are well-marked Linnean species, it was perhaps very definite also, the principle of divergence of character coming into operation.

Another well-known series of facts is that families which are widely distributed chiefly or only in the more broken southern hemisphere, have rarely any genera that cover the whole of their area of distribution. In the plants that are more marked in the northern hemisphere, on the other hand, there is very often a genus that does cover the whole area, even if that also includes the southern hemisphere, such for example as *Ranunculus*, *Senecio*, or *Solanum*. Whether this difference has anything to do with the isolation of so many areas in the south, we do not know, but the fact is suggestive.

We are still very far indeed from any proper understanding of the operations that have been concerned in evolution, except that natural selection must evidently play a less conspicuous, or at any rate, a less direct part. It looks as if, more especially under certain circumstances such as elevation or isolation, evolution must go on, and this supposition is borne out by such things as the progressive change that shows in such plants as *Stratiotes* described by Miss Chandler (3), where a whole series of species differing in characters of no conceivable functional importance, have succeeded one another in successive geological horizons. If these changes had been a little more marked, we should have had two or more genera succeeding one another, and this point must always be borne in mind, together with the tendency to divergence, in considering extinct genera.

CHAPTER VIII

DIFFERENTIATION

WITH his customary scrupulous fairness, Darwin went out of his way to draw attention to an axiom of taxonomic botany that was seriously opposed to the theory of evolution by adaptation through the agency of natural selection. "Those classes and families which are the least complex in organisation are the most widely distributed, that is to say that they contain a larger proportion of widely distributed species." Incidentally, as the simpler families must upon the whole be the older, this goes a good way towards proving the correctness of the theory of age and area.

Now upon the theory of natural selection, it is clear that the successful genera must be those that have the largest numbers of species, or the widest distribution, or both; but as they have been developed by adaptive selection, they should surely on the whole be the most complex and specialised, showing the most signs of adaptation. This has always been a difficulty to the supporters of natural selection, and one which has been passed over with little remark. It can be at once explained by the hypothesis brought forward in *Age and Area*, for upon that the older forms will be the more widespread, and by reason of their age they must be the simpler on the whole, as having been more early formed in the process of evolution. But age and area is incompatible with the theory of natural selection.

Age and area leads on directly to the theory which Guppy has called Differentiation, though a simpler and better descriptive term might perhaps be found—mutation perhaps, or differential or divergent mutation, for example, if it were admitted that mutations might be large. The essential feature of the theory, originally adumbrated by Geoffroy St Hilaire (41), is that evolutionary change goes downwards *from the family towards the species*, not in the opposite direction. A family begins as a family, and is not gradually formed by the destruction of intermediates. At the same time, of course, when it begins it is also a genus and a species, which at the start are all-important to the family; if the species be killed out, the family disappears. As it grows, the single genera and species become less important to it. The name

differentiation was given by Guppy (11), whose concept it was that in the far back days of damper and more uniform climate most of what are now the large (or widespread, or both) families were formed, each at one stroke by well-marked mutations, and they then slowly began to grow in size by further mutations. As time went on, and the earth perhaps became drier on the whole, the variety of climate would increase, and mutations perhaps be more rapid, but their "size" is supposed to have become less, so that fewer great divisions, like for example the Monocotyledons, tended to appear. As differentiation went on in the climates, so it went on in the living forms. This does not mean that they were necessarily formed in adaptation to the climates but rather perhaps that the climatic change gave the stimulus which resulted in further mutations. Mutations might be of any rank, from variety up to division, so that any difference might appear at one stroke. If the newly formed plant could pass through the sieve of natural selection, and escape the dangers that threatened its very existence when it first began, it might then begin to spread, and once established in several places it would be, comparatively speaking, safe. As the original species thus survived *as well as* the offspring, the family must necessarily increase in number in such a way that when plotted by their numbers of species, its genera would form the "hollow" curve. It is quite possible that after a certain lapse of time a species *must* die out (43), and it is still more possible that it may change into another by some simultaneous mutation. We have seen a small instance of simultaneous mutation in the sudden loss of smell that happened to all the plants of musk some years ago, and may perhaps see the results of series of such mutations in the consecutive species of *Stratiotes* described by Miss Chandler (3) and other such series.

While under natural selection new forms only arise as the result of improvements in adaptation, under differentiation they arise because evolution must go on, at any rate whenever the needful stimuli, or conditions, are present, as we have seen in the case of the Podostemaceae (p. 20). Under natural selection the small variety becomes a larger one, and so on. It seems to the writer, as it did to Dr Guppy, that in trying to make evolution work in this way, people have been trying to work it *backwards*, and it is with the object of showing the necessity of proper revision of the current view that the present book is written. A number of more or less crucial test cases are given below, all of

which seem to point to the supposition that differentiation gives a more correct picture of the direction of movement of evolutionary change than does natural selection, even though we have no clear vision of the mechanism that was involved in making the changes that occurred.

The family is supposed to have arisen by some well-marked and sudden mutation (or conceivably a series of smaller ones, probably at close intervals), which would at one stroke change two or more characters and pass the line of mutual sterility that commonly divides species from one another. As the characters that divide the families are, after all, not so very numerous (cf. Appendix I) each family must take a different combination, sometimes taking one of a given pair, sometimes the other, and in every kind of mixture. Many families, for example, have alternate rather than opposite leaves, or superior rather than inferior ovary, but only the Cruciferae have alternate exstipulate leaves, bractless racemes of ♀ regular flowers, sepals in two whorls of two, four petals, two short and four long stamens, superior ovary of two carpels, unilocular with replum, a pod-like fruit, and exaluminous seeds. As the characters run in contrasted pairs (or triads), we have no information as to whether there is any advantage in one side rather than the other, or in either as against any possible intermediate, or indeed that any has any adaptational value. There is thus no evidence to show in which direction evolution moved, and we are perfectly free to select that for which we think that the evidence is better. It is this evidence, or rather, some of it, which we propose to bring forward below.

Nor can we say with any likelihood of accuracy that the change indicated in any one pair is larger than that in another. Is it a greater change from two cotyledons to one than from alternate to opposite leaves? We do not know; all we have to go upon is that the latter is much more common. With one or two rare exceptions, there is no difficulty in supposing all Monocotyledons to have descended from at most a few different ancestors, whilst one may find alternate and opposite leaves side by side in many cases of allied genera or species. There is nothing inherently absurd in the idea that a family might be founded by a single mutation.

About 1902 the writer became a convert to the theory of mutation, but it seemed to him completely illogical to insist that mutation could only be very small, when before us, in every

family, there lay so much evidence that species, genera, tribes, sub-families and families were so continually separated by such well-marked divergent characters as leaves opposite or alternate, anthers opening by slits or by pores, ovules 1-2-∞ in each loculus, raphe dorsal or ventral, and many more such differences, which allowed of no intermediate or transition forms upon which natural selection might operate, which were such that one could not conceive of natural selection choosing between them, and which were so constant in their morphological character—a feature that one could not expect natural selection to bring forth. They could only, it would appear, be the result of definite single mutations, and therefore mutations must at times be large. And if large in regard to these characters, which are very often of “family” rank, why not in all cases?

In May 1907, without having seen Dr Guppy's book, the author published what was essentially the same theory (70), largely based upon the study of the Podostemaceae, and upon ten years' experience of tropical vegetation. Both authors were convinced that the great importance at that time attributed to adaptation was exaggerated. Natural selection was trying to construct a tree from the twigs downwards. But though a tree grows from the ground upwards, it always has young twigs and leaves (which may be looked upon as representing genera and species), though *each one, when the tree is small, has a much greater value in proportion to the whole organism than when the tree is large.* It seemed to us clear that in trying to show that evolution proceeded in the order

Small variety—Large—Species—Genus—etc.,

people were trying to make it work backwards, and that the proper order was

Family—Tribe—Genus—Species—Variety.

The relative rank of these groups varied as time went on. When very young, the family, the genus, and the species were the same, but as the family grew in size (just as with the tree mentioned above) the species became of less and less relative rank when compared to it.

To turn to geographical distribution; upon the theory of natural selection, the large and widely distributed genera are the successes, the small and local the failures or relics. The success was always put down to better adaptation to conditions, though no one tried to explain how a species that derived its adaptation,

say, in Europe, was able to spread as far as New Zealand. It could not become, in Europe, adapted to the conditions of New Zealand, and its appearance there must be due simply to the chance that the conditions resembled one another in both places, and that there were conditions in between that were not dissimilar at the time that the plant reached them. There can be no doubt that as a plant moves very slowly about the world, it can become adapted as it moves to the slightly different conditions that occur at each move. If it come to a place where the change is too sudden for it to adapt itself, it will then have come against a barrier to further spread—an ecological or a climatic barrier, to be added to the barriers of physical nature, such as high mountains, or open seas, that so often occur. By the formation of one of these barriers after the plant has passed, the distribution of a species may become discontinuous.

The success of a species under natural selection means usually the greater or less extermination of the one from which it descended, and which was not so well adapted. Under the theory of differentiation, on the other hand, which goes with that of age and area, the large and "successful" genera are simply the oldest, while the small and local are in general the youngest. There is no special adaptational reason for size or spread, so that, within any close circle of relationship (which will more or less ensure the same general reactions to the outside world), the rate of spread of two or more forms will not usually be widely different. This is the essence of the theory put forward in *Age and Area*.

In diagram 7 we have indicated what we imagine to be the probable general course of evolution under the theory of differentiation. The family is represented at the start by a solitary monospecific genus *A*, which will throw off new forms by mutations. At first they will probably be produced very slowly indeed, but as *A* increases its numbers (and with them its area, thus probably coming under the stimulus of different conditions) will probably appear more rapidly. Whether the earliest mutations will be more often specific or generic we have no idea, but most probably a second genus *B* will be "thrown" before so very long a time. This will again begin slowly, and it will be a long time before it throws a new genus *Bb*, whereas *A* will probably throw its second new genus *C* before *Bb* appears. All this, of course, is dealing in averages, and we do not know that this particular *B* will necessarily be slower than *A*, though on the average the second genus will be behind the first throughout. On the average

A, as the oldest genus, should have the greatest area and the greatest number of species, *B* the second, *C* the third, *Bb* probably the fourth, and so on, but only on averages. Whilst in Ranunculaceae *Ranunculus* has 325 species to 250 in *Clematis*, one would hesitate, and rightly so, to say that the former was the older, when one remembers that it is herbaceous, and *Clematis* shrubby.

As time goes on, it is clear that the rate at which new genera

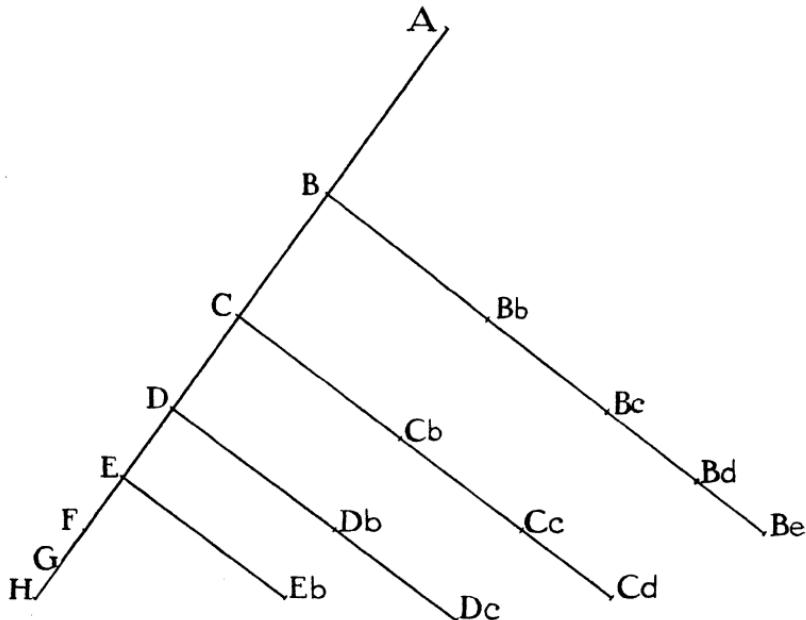


Fig. 7. Evolution by differentiation. Each genus is supposed to survive the whole way along the line at right angles to its origin, e.g. *A* still survives at *H*, *B* at *Be*, and so on. In order to save complication, the lines to show the growth *Bb*, *Bc*, &c. are not shown.

are formed will increase. Each genus will begin with one species, and after a time will form more, so that the few older genera of the family will contain the greatest numbers of species. The result will be (cf. 66, p. 185) the gradual formation of the familiar hollow curve already described, with a few large genera of different sizes at the top, and many monospecific genera at the bottom, the numbers increasing from top to bottom at an accelerating rate. As there will rarely, upon this theory, be any appreciable adaptational difference between species or even genera, there will be little or no reason why the older ones should be killed out (as there is under natural selection), and so the increase in numbers will lead inevitably to the hollow curve.

Up to the present, this theory is the only one which can make any pretence of explaining the hollow curve. The latter is so universal that it is evidently a general law which must be explained. But it is, of course, in direct contradiction to the theory of natural selection. With the latter theory one can make no predictions as to what may be found in the arrangement and characters of families, genera, or species. With differentiation one can make a beginning in this direction, and this alone makes a strong claim in its favour.

If differentiation be the rule, it is clear that the ultimate result of the growth of a family from one original genus *A* to a fair number of genera should in general be the formation of groups within groups, like the cat group or the dog group within the larger group of Mammals. By the principles of differentiation and of divergence of variation, each genus thrown will tend to be markedly different from the parent that throws it. If it were thrown very far back in the history of the family, it will have had time to throw more genera in its turn. These may, but so far as one can see, not necessarily must, display the character or characters that made their parental genus, *B* for example, different from its own parent *A* upon the main line of the family. When these genera upon the second line *B* had become more or less numerous, or in any case if the characters of their parent had included two or more of the characters which we usually rank as "family" characters, they would form a group *Bb*, *Bc*, *Bd*, etc., well marked off from the first group which was being formed by the genera upon the main line, *A*, *B*, *C*, *D*, etc., and to these two groups we should probably give the rank of sub-families, or tribes, according to our conception of the value of their characters. One of these groups would most probably be larger and perhaps more widely dispersed than the other, and both would continue to grow and to spread. Supposing that the family escapes without very great damage all the various accidents that may befall it, and that all its genera behave fairly closely in the same way, as would be the case under differentiation, the original parent *A* will have the largest number of species (theoretically) and the largest area of occupation, while the other genera, *B*, *C*, etc., will be successively smaller in these respects, as we have seen in the Monimiaceae for example. The difficulty in defining what is or is not a sub-family or a tribe is the same as that of defining a genus or a species. We have no standard to work by in defining the value of a certain character, other than the way in which it

appears in the group under consideration. Ruminate endosperm being characteristic of all Annonaceae, and of none of the allied Magnoliaceae, becomes very important in regard to these two families, while in the palms, etc., it may characterise some only of the species of a genus. Upon the theory of differentiation this, of course, simply means that in the one case the ancestor that showed it was the ancestor of a whole family, in the other only of a few species. Any of those characters which we usually consider as especially "family" characters may appear at any stage from family down to species, but on the whole are more common as one goes upwards in a family from the species.

One thing that is always brought up as an argument against those who object to the explanation of evolution by natural selection is that the fossil records show many extinct genera, of families still existing. The theory of natural selection, based upon adaptation, with its prompt killing out of less-adapted ancestors, accounts easily for this, while differentiation, which supposes the ancestors to live on together with their descendants, cannot do so. But one is apt to forget that the explanations of the facts of palaeobotany have for many years been such as could be made to fit with the all-powerful theory of selection. One is reminded of the defence of phrenology in *The Professor at the Breakfast Table*. There are a number of things that must be taken into consideration before one can fully explain the fossil records.

In the first place, it seems not impossible, as Small has shown (48), that there may be a definite limit to the life of species and genera. In his summary he says: "From this the important deduction can be made that species die a normal death, presumably from the senescent sterility of old age, with, perhaps, a minor part being played by the progressive restriction of survival conditions for a senescent species . . . the species number in a genus is shown to follow the series

1-2-4-8-16-32-44-43-41-37-29-18-0.

This gives 24 million years as the normal lifetime of an ordinary genus."

This is supported by such facts as those brought out by Miss Chandler (3), who found in different recent horizons a whole series of fossil species of *Stratiotes*, differing structurally from one another, but with nothing to which one could possibly attribute any adaptational value. The loss of smell by musk (p. 66) shows that a whole species can undergo a simultaneous change; a larger

mutation than this might have changed the whole of it to another species. Then again, if a geological catastrophe come along, it may easily destroy a whole species, or even genus, that has not yet been able to spread far enough to get beyond its range. Unless a fossil is found to cover such an area that it is unlikely that such a fate may have overtaken its living representatives, it seems to the writer in the highest degree unsafe to look upon it as an ancestral form of existing species. It is more likely to be a lateral mutation thrown off from the main line, and exterminated as a genus by some happening.

Lastly, there should be mentioned the all but complete absence of transition stages in the fossils, a fact which violently disagrees with the supposition that evolution was gradual and continuous.

CHAPTER IX

DIVERGENCE OF VARIATION

IT has long been known, though it has excited but little interest, that there is a great tendency in variation to be divergent. As Guppy says (66, p. 104) Hooker, in his lecture upon Insular Floras, "shadowed out a general notion of Centrifugal Variation operating through countless ages". It appears almost as a suggestion, but the idea had been evidently floating half-formed in his mind ever since he wrote his essay on the Tasmanian flora in the late 'fifties. It was the nucleus of a theory of Divergence or Differentiation that acquired more definite outlines as time went on, since it reappears in the intensely interesting account of a talk with Darwin which is given in a letter to Huxley in 1888 (19, II, p. 306).

"We can perhaps understand the long intervals of time now. For the confirmation that such a theory would have derived from a line of research instituted on Darwin's lines was denied to him. The two proved to be incompatible. For no inductive process based on Darwin's lines could have found its goal in a theory of centrifugal variation. 'I well remember', Hooker describes in a letter to Huxley in 1888, 'the worry which that tendency to divergence caused him (Darwin). I believe I first pointed the defect out to him, at least I insisted from the first on his entertaining a crude idea which held that variation was a centrifugal force, whether it resulted in species or not.' Huxley was in the same case. For he held views of the general differentiation of types, and his road that would lead to the discovery of the causes of evolution started from the Darwinian position. That road was barred to him."

There can be no doubt, when one looks at the various characters that are used in taxonomic distinction between one form and another, that the bulk of them are divergent, and that the more so the higher one goes in the tables of characters, upwards from species to families. Take for example the list of "family" characters given in Appendix I, and note the great proportion of distinctions in which there cannot even be an intermediate, by reason of the marked divergence, and where, in any case, there can be no functional difference between the intermediate and the

two extremes. For instance, among the characters will be found the following:

- Root tap or adventitious
- Stem monopodial or sympodial
- Leaves alternate or opposite
 - simple or compound
 - palmate or pinnate
 - parallel or net veined
- Inflorescence racemose or cymose
- Flower spiral or cyclic
 - mon- or di-oecious
 - iso- or hetero-merous
 - regular or zygomorphic
- Receptacle above or below calyx
- Parts of flower in 2s, 3s, 4s, 5s, etc.
- Calyx in one or two whorls
- Odd sepal anterior or posterior
- Corolla free or united
 - imbricate, valvate, or convolute
 - alternate with, or superposed to, sepals
- Stamens in one, two, or more whorls
 - diplostemonous or obdiplostemonous
 - free or united
- Anther versatile or not
 - opening by slits, pores, valves, etc.
- Pollen in various patterns of cell wall
- Carpels free or united
 - 1 to ∞
 - transverse or anteroposterior
- Placentation parietal, axile, etc.
- Raphe ventral or dorsal
- Micropyle up or down
- Style basal or terminal
- Stigma capitate or lobed
- Fruit achene, follicle, capsule, drupe, berry, etc.
- Seed with or without endosperm
 - one, few, or many
- Embryo straight, curved, twisted, etc.

and many more equally divergent, whilst in the few cases where intermediates are possible, no functional value or disadvantage can be read, either into them or into one of the extreme divergents. In no case, in these family characters, has any functional value been shown, in a definite and unmistakable manner, though suggestions have been made in one or two cases.

If now one go on to the characters used in the keys which determine the genus and species of a plant belonging to one of

these families, one finds the same kind of divergences, more and more marked on the whole in approaching the top of the list (the first divisions in the keys), and least marked in the characters that distinguish one species from another. This fact of increasing divergence as one gets nearer to the top of the list has always been a great difficulty in the path of the supporters of natural selection, and has been left discreetly unmentioned by them.

Opening a volume of Engler, the family displayed is the Cyclanthaceae, composed of six genera only. The first and most obvious division, into Carludoviceae with male flowers in fours, and Cyclantheae with male and female flowers in alternating rings or spirals, picks out the two most important genera, one in each of the groups, though the first group, with five genera and forty-five species, is much larger than the second, with one and four. Incidentally, how did selection, or gradual adaptation, produce these two very distinct types of inflorescence, and what was intermediate between them? Taking first the Carludoviceae, the genus *Ludovia*, with two species in Guiana and Amazonas, is first cut off, having only a rudimentary perianth in the male flower (why, on the theory of selection, did it spoil its attractiveness to insects?). The four genera left are divided into *Carludovica*, which has forty species covering the whole range of the family in tropical America (north and south) and the West Indies, and which has a short perianth in the female flower, against a long one in the other three (again, attractiveness apparently spoiled), and an inferior ovary against a superior. *Carludovica* is by far the largest genus in the family, far outnumbering all the rest put together, and has a distribution covering that of the whole family, just as we have seen to be a general rule (p. 64). Does it owe its "success" to its inferior ovary, and if so, wherein does the advantage lie, for the flowers are so crowded that one cannot tell from the outside that the ovary is inferior? And if there is an advantage there, what about the reduced perianth?

Evodianthus, next, is distinguished from the two other genera by having the stamens inserted in the tube of the perianth, while the others have them on the disk; and finally *Stelostylis* has the stalk of the male perianth flat and hollow, and a pyramidal style, while *Sarcinanthus* has the male perianth forming six-sided pyramids, and no style. All three are small and little dispersed genera with two species in Costa Rica and the West Indies, one in eastern Brazil, and one in Costa Rica, respectively.

Cyclantheae has only one genus, *Cyclanthus*, with four species in tropical South America from Peru northwards, and in the West Indies. It is thus the second genus of the family both in number of species and in dispersal, but as it is so much smaller than *Carludovica*, we must suppose that it was only cut off from that genus rather late. Its dispersal is much smaller than that of *Carludovica*.

There is no reason for supposing the small genera to be reliques; it is far simpler to imagine them all split off by large mutations from *Carludovica* in its gradual dispersal over the whole area of the family. The first split probably gave *Cyclanthus*, which is the second largest genus, and has a division to itself in the family, whilst it would seem extremely probable that the mutation that gave rise to it was an extra "large" one, for the difference is so great between it and the rest. The other four genera, smaller, and with less distribution, count in the same group with *Carludovica*, from which they are not so markedly different. The general impression that one gains here, as in almost all cases, is that after the big mutation which first gave rise to the family, there followed others which gradually became less and less marked, and which kept more or less closely within the boundaries that were indicated by the first mutation that occurred after the formation of the family.

The first impulse of many will be to say that Cyclanthaceae form an exceptional family, and perhaps also to say that the keys are artificial things. But the exceptional families, and the divergences that are shown in the keys, have both to be explained by natural selection, or by any other theory of evolution, just as much as have the ordinary families and the smallest divergences. Natural selection would be very hardly pressed to find any explanation of the very remarkable differences between *Carludovica* and *Cyclanthus*, especially as it is all but impossible even to imagine that there can be any intermediate stages, and no use-value can be put to either of the extremes or to any conceivable intermediate.

This supposition, that the first mutation, in a family newly formed by a large change from some ancestral form, may be in turn large, is well supported by an examination of the keys to the various families that are given in any general text-book of systematic botany. In the list in Appendix II, I have extracted from the keys in my *Dictionary*, 6th ed. (which are mostly taken from the *Natürlichen Pflanzenfamilien*), the first dichotomy in

each case, omitting a few keys where the first break is into three or more. These sixty families of course were selected for the *Dictionary* as being the larger or more important, and we shall go on to deal with the smaller ones below.

It will be seen at once that these are characters the bulk of which are of the same rank as the "family" characters given in Appendix I. To take a few examples, one finds among them such character-pairs as these, which can all be matched in the family characters:

1. Leaves opposite—alternate	Gentianaceae
2. Leaves in two ranks—not	Musaceae
3. Inflorescence racemose—cymose	Verbenaceae
4. Flower naked—with perianth	Betulaceae
5. Perianth actinomorphic—zygomorphic	Campanulaceae
6. Calyx polysepalous—gamosepalous	Caryophyllaceae
7. Calyx valvate—imbricate	Mimoseae (Legum.)
8. Stamens free—in tube	Meliaceae
9. Stamens two—one	Orchidaceae
10. Carpels free—united	Annonaceae
11. Carpels six to fifteen—three to five	Hydrocharitaceae
12. Ovule one per loculus—two	Euphorbiaceae
13. Fruit a berry—loculicidal capsule— septicidal capsule	Ericaceae
14. Fruit many-seeded—one-seeded	Myrsinaceae
15. Fruit achene—follicle	Ranunculaceae

Incidentally, how does natural selection account for, or explain, the differences shown in 2, 3, 6, 7, 9, 11, 12, 13, 14, 15, to say nothing of the others?

If one go on to the second dichotomy in a key to a big family, one finds that there are on the whole fewer, though still some, of the "family" differences shown, but these become less frequent in proportion to the total, as one goes down the list.

It might be thought, perhaps, that small families would show a difference from the larger ones, possibly in having smaller divergences in their classification into genera. If they were really relictas, as they are often supposed to be, this might be the case, but in actual fact it is not found, as a glance at Appendix III will show. This contains the distinguishing characters of the genera in the families that contain two only. Here again one finds such distinctions as:

Leaves opposite—alternate	Caryocaraceae Erythroxylaceae Trigoniaceae
---------------------------	--

Perianth five—four	Achatocarpaceae
Flower 5-merous—3-merous	Limnanthaceae
K and C alternate—superposed	Caricaceae
Corolla valvate—convolute	Quiinaceae
Corolla free—united	Xyridaceae
Stamens few—∞	Salicaceae
Carpels two—three	Balanopsidaceae
Capsule—berry	Balsaminaceae
	Taccaceae

It is clear that in these small families the first split, which is only into two genera, shows just as important divergences as does the first split in the large families, which is into two sub-families, and the two genera of the small family are just as well separated as are the two (average) largest genera of the big family, which head its two chief sub-groups. The importance of this fact we shall better appreciate when we return to its discussion in the Test Cases (below, p. 112). If small families really consisted of relics, one would not expect that their genera should be divided by divergences of any special size, and certainly not that the divergences would be of the size and form that one expects to find between the sub-families of large families, or even between the large families themselves.

If one take a number of monotypic families, or families of one genus, from the first edition of Engler, and look at the distinctions there given for dividing the species of each of the genera into two chief groups, one finds these characters to be of some systematic importance, and often to be characters that are not, or hardly, capable of having intermediates. It is very hard to see how characters of such divergence should be those supposed to be left in the genera that survive of what is supposed to be a dying family. Here are a few examples:

Monocotyledons.

Typhaceae. Fruit with longitudinal groove, and opening in water; seed not united to fruit wall.

Fruit without groove, not opening in water; seed united to fruit wall.

Sparganiaceae. Inflorescence branched.

Inflorescence not branched.

Naiadaceae. Dioecious. Stem and back of leaf spiny.

Testa of many layers of cells.

Monoecious. Stem and back of leaf not spiny. Three layers.

Cannaceae.	Three outer staminodes separate. Two outer united, third free.
Dicotyledons.	
Casuarinaceae.	Twigs whorled, rarely 4-angled, and then hairy in fork. Twigs not whorled, or 4-angled with whorls of four leaves.
Myricaceae.	Female flower with two to four or more bracteoles, not accrescent to fruit. Female flower with two lateral bracteoles, accrescent to fruit, making two wings.
Myzodendraceae.	Male flower with two stamens. Male flower with three stamens.
Grubbiaceae.	Flowers in threes in axils of foliage leaves. Fruit hairy. Flowers in threes in axils of opposite bracts. Fruit not hairy.
Ceratophyllaceae.	Fruit without spines or wings. Fruit with spines or wings.
Moringaceae.	Seed without wings. Seed with wings.
Nepenthaceae.	Seeds egg-shaped with no appendages. Seeds with long hairlike coat.
Myrothamnaceae.	Two bracteoles. Stamens free. No bracteoles. Stamens in column.
Platanaceae.	Leaves usually 5-nerved. Leaves usually 3-nerved.

Both in the monotype and the ditype families it will be seen at once that the characters that distinguish the species in the one and the genera in the other, are of the "family" type rather than of the specific or generic type found in large families. And most often they allow of no intermediates. Nothing but divergent mutation will explain such things.

It is fairly clear that the larger genera tend to head sub-families, or groups of whatever rank may be considered appropriate in the family concerned. It will therefore be of interest to study one or two families in greater detail, and the first that comes up in a random choice is the Ranunculaceae. We shall expect, upon the theory of differentiation or divergent mutation which we have been discussing, that the chief division in the key will usually lead to the two chief groups into which the family is divided, and that each of these will be headed by one of the two

or three largest genera in the family. Of course, since we cannot be sure of what is the largest divergence, nor be sure that that divergence necessarily came first in the mutations, we shall not expect every family to show such a result with any certainty, though one may expect it to show more often than not. The important point is that each sub-group should be headed by a comparatively large genus. If the group be small in proportion to the family, the genus may be small in proportion to some of the largest genera of the family; if large, one will expect its leading genus to be larger.

We shall further expect to find the smaller genera practically all included in the key that is marked out by the first divergent mutation. That is to say, that we shall in general expect them to be grouped as satellites round the big genera, not, as one might expect if they were relics, in small and comparatively isolated groups, which need not necessarily be closely related to the big groups of the present day. We shall, therefore, expect the characters of these small genera to be less and less marked the smaller (by the number of species in them) that they are, and to be, so to speak, squeezed in between the well-marked characters of the large genera. Real relics, on the other hand, would be more likely to be distinguished fairly clearly from their relatives of the same family, by characters that might even be as marked as those that show in the first or second dichotomy of the key.

The Ranunculaceae, a family of medium size, not very much larger than the average size for all families, have seven genera that (in comparison with the rest of the family) we may call large, each one containing at least seventy-five species. There are nine of intermediate size with ten or more, but none exceeding twenty (figures some years old), and ten small with nine or less. This gap between the large and the intermediate genera is not an uncommon occurrence, especially in families of small and medium size, and should be well worth further investigation.

The big genera are:

	Spp.	Belonging to group
<i>Aconitum</i>	150	A 2
<i>Anemone</i>	180	B
<i>Aquilegia</i>	75	A 2
<i>Clematis</i>	250	B
<i>Delphinium</i>	175	A 2
<i>Ranunculus</i>	825	B
<i>Thalictrum</i>	75	B

Total 1180 or 87 per cent of the family

The intermediate genera are:

<i>Actaea</i>	15	N. temp.	A 2
<i>Adonis</i>	10	N. temp. Old World	B
<i>Coptis</i>	10	N. temp. and Arctic	A 2
<i>Caltha</i>	20	Temp.	A 2
<i>Helleborus</i>	15	Eur., Medit. region	A 2
<i>Isopyrum</i>	20	N. temp.	A 2
<i>Nigella</i>	16	Eur., Medit. region	A 2
<i>Paeonia</i>	15	Eur., Asia, W.N. Amer.	A 1
<i>Trollius</i>	12	N. temp. and Arctic	A 2

Total 133 or 10 per cent of the family

The small genera are:

<i>Anemonopsis</i>	1	Japan	A 2
<i>Callianthemum</i>	5	Mts. of Eur., C. Asia	A 2
<i>Eranthis</i>	7	N. temp. Old World	A 2
<i>Glaucidium</i>	2	Japan, China	A 1
<i>Hamadryas</i>	4	Antarctic Amer.	B
<i>Leptopyrum</i>	1	C. Asia	A 2
<i>Myosurus</i>	7	Temp.	B
<i>Oxygraphis</i>	9	N. temp. Asia and Amer.	B
<i>Trautvetteria</i>	6	Japan, N. Amer.	B
<i>Xanthorrhiza</i>	1	Atl. N. Amer.	A 2

Total 43 or 3 per cent of the family

Grand total 1356 spp. in 26 genera, average 52.

The classification used here is that of Engler and Prantl, in their first edition—Paeonieae (A 1) and Helleboreae (A 2) being marked off from Anemoneae (B); Paeonieae have only two genera. Of the large genera given above, three belonging to group A 2 have an average of 133 species per genus, and are only North temperate in distribution, while four belong to group B, average 195, and are cosmopolitan in distribution in three cases, the fourth being only North hemisphere. On the face of it, by the greater size and greater distribution, B would appear to be an older group than A. The intermediate genera are intermediate both in size and in distribution, and the small genera are evidently the lowest in both respects.

Now the very old and large genera, upon the theory of differentiation, must owe their origin to the earliest generic mutations in the family, and upon the principle of divergence of variation, we shall expect these variations to be, on the whole, the most divergent that occur in the family. In other words, the larger genera of a family should be separated by well-marked divergences, while the smaller will be less so. This is exactly what

we do find. If we draw up a key to the Ranunculaceae, dealing only with the seven big genera given in the list above, it will be found to be just such a divergent key, so that to place a species in its proper genus is a very simple matter. Here is the whole key:

A. Ovules on both sides of ventral nerve of carpel: follicle—

Flower with 2 or (2) honey-leaves:

Honey-leaves sessile, odd leaf of
perianth spurred, projecting.

Delphinium

Honey-leaves stalked, odd leaf
helmet-shaped, erect.

Aconitum

Flower with 5 honey-leaves.

Aquilegia

B. Ovule solitary at base of ventral nerve: achene—

Ovule with one integument.

Ovule pendulous:

Leaves opposite.

Clematis

Leaves alternate (exc. involucre).

Anemone

Ovule erect.

Ranunculus

Ovule with two integuments.

Thalictrum

The key is a very simple affair, with widely divergent characters at every stage, so that there can be no difficulty whatever in placing any species in its genus, were these the only genera in the family. It is only when the smaller genera are included that any difficulty is found. With each new one that is added, the characters that have to be used become more numerous and more complicated. These seven large genera cover practically the whole range of variation that is found in the family, to say nothing of including 87 per cent of the whole, and the rest of the genera come within, or very close to, the range thus indicated. If one add to the seven large genera the rest of the family, which consists of small genera not exceeding twenty species, one finds that the steps which in the above key lead only to *Ranunculus* lead also to *Myosurus*, *Oxygraphis*, *Trautvetteria*, and *Hamadryas*. A whole series of new steps in identification is now required, but the important and interesting point is that all the new additions come within the original key, or very nearly so. The new additions that have to be made to the lists of characters are all at the generic end of the key or close to it, with few exceptions. Instead of finding that "ovule erect" leads straight to *Ranunculus*, we have to have a supplementary key like the following:

(Ovule erect)

Flower hermaphrodite.

Fruit with no hard layer in wall.

Ovule ultimately pendulous; perianth leaves spurred.

Myosurus

Ovule always erect; perianth leaves not spurred:

With honey-leaves.

Oxygraphis

Without honey-leaves.

Trautvetteria

Fruit with hard layer in wall.

Ranunculus

Flower dioecious.

Hamadryas

While almost all of the new and smaller (younger, according to age and area) genera that have to be added to the key that we obtained from the large (old) genera are added simply in such a way that they cluster around some of the big genera, like those just given cluster around *Ranunculus*, one finds every now and then one or more genera (usually clustered) which do not so obviously represent satellites of the big genera, but have a focal point of their own. Thus among the intermediate genera in Ranunculaceae there appears *Paeonia*, whose characters require a splitting of the early character of distinction given above and marked A. Instead of leading directly to *Aquilegia*, *Delphinium*, and *Aconitum*, as at present, A has now to include *Paeonia*, which cannot be easily split off, as was *Ranunculus*, by extension of the generic end of the key, but has to be split off as follows:

A: Follicle, etc.

Outer integument of ovule longer than inner; *Paeonia*
no honey-leaves; ovary wall fleshy.

Outer integument not longer, sometimes one *Aquilegia*, etc.,
integument only; honey-leaves or not; as before
ovary wall rarely fleshy.

Passing yet further down the scale of genus-size, *Paeonia* becomes accompanied by *Glaucidium*, with two species in the mountains of Japan and China (a much smaller distribution than that of *Paeonia*, as one would expect upon age and area). As the separation of *Paeonia* was so comparatively high up in the scale, this small group of two genera is evidently of somewhat different rank from that which surrounds *Ranunculus*, and is often regarded as a sub-family; but it is important to notice that it is hardly of the rank of the other two sub-families. As a key to the three sub-families, we have

- A. Ovules on both sides of ventral nerve; follicle—
- | | |
|---|--------------------------|
| (1) Outer integument of ovule longer. | Sub-fam. I. Paeonieae |
| (2) Outer integument of ovule not longer. | Sub-fam. II. Helleboreae |
- B. Ovule solitary at base ventral nerve; achene. Sub-fam. III. Anemoneae

As *Paeonia* is comparatively small, it is extremely probable that it is much younger than the Helleboreae, which include three of the first seven very large genera; and this is confirmed by its small distribution as compared with them.

It is clear that if we suppose the big genera of a family to be the first formed, and that by the most divergent variation that (on the whole) occurs in the family, whilst the intermediate and smaller genera are younger, we can get a satisfactory picture of what seems to have gone on. The big genera, formed by early and divergent variation, mark out the outer limits (or nearly so) of the family, the intermediate and small ones, which are on the whole the younger, coming later and filling in the outline thus made. In the later stages of the family, the divergences tend to become smaller and smaller, especially as the possibilities of large divergences have become somewhat used up. At each stage the divergence is probably limited by what has already occurred, and with comparatively few exceptions keeps within the limits thus marked out. If, as in Annonaceae, the commencing mutation, which gave rise to the family, includes a berry fruit, then this may be a family character; if, as in Myrtaceae, it is produced in the second mutation, the berry may characterise the sub-family resulting from that. It may even be produced in later and later mutations, and be the mark only of a tribe, a sub-tribe, a group of genera, a single genus, or it may even mark only some of the species in a genus.

The key to a family, if well constructed, in all likelihood gives a clue to the mutations by which that family evolved into its present condition. But one must remember that while a group of the largest genera will doubtless be older than a similar group of smaller ones in the same family, those that are actually largest, or those that are the most widely distributed, need not necessarily be the oldest, for there are so many accidents that may befall plants in the shape of geological and other changes. Once a genus becomes so large and important that it has many species and

covers great areas, the chances of its complete disappearance, unless mere age, or further (probably universal) mutation can do it, are small. The intermediate genera, on the other hand, may often have suffered complete extinction, and still more the smallest genera.

What has been said is also strongly supported by the facts of distribution. There can be no doubt that in any given family, the distribution of the genera goes on the whole with their size, as has been shown in *Age and Area*, chap. xii, p. 113 (Size and Space). Age, size of genus, and area occupied by it, all go together.

It is clear that this analysis of the Ranunculaceae fully supports the theory of differentiation as against that of natural selection, upon which no prediction can possibly be made as to the size or composition of a family.

As another example, let us take the sub-family Silenoideae in the Caryophyllaceae. It contains eighteen genera, whose numbers of species, from the latest monograph (35), where the numbers in the large genera are evidently rounded off, are

400, 300, 90, 80, 30, 30, 25, 10, 8, 7, 5, 5, 4, 4, 4, 1, 1, 1.

The first two genera, *Silene* (400) and *Dianthus* (300), which contain 700 out of the total number of 1005 species in the sub-family, are instantly picked out (supposing these to be the only genera in the group) by the very first dichotomy that is given in the key, which splits the Silenoideae into two tribes. All the Lychnideae, headed by *Silene*, show a calyx with commissural ribs; the Diantheae, headed by *Dianthus*, not so. The other Lychnideae contain 80, 10, 8, 7, 5, 5, 4, 1, 1 species, and the other Diantheae show 90, 30, 30, 25, 4, 4, 1, adding up, the one to 121 species, the other to 184, or in both cases much fewer than in the big genus at the head of the group (400–121 and 300–184). Each tribe is headed by a big genus, and the one tribe adds up to 521, the other to 484, showing a difference just as indicated in Test Case II, p. 94. The figures seem to indicate that in the Diantheae there were more genera produced of intermediate size, so that perhaps the stimulus of genus formation came earlier, and resulted in the greater number of species shown by the smaller Diantheae than by the smaller Lychnideae.

As the divergence just considered includes all the Silenoideae on one side or the other, it is not unlikely that it was the first mutation to appear after the first formation of the group by the

mutation that produced *Silene* itself. All later mutations come within it, in the sense that the effects of this first mutation are shown in them all. If we now follow only the tribe Lychnideae, Pax's key next splits off, by triple (or more probably by two separate) divergences two genera, *Cucubalus*, with one species in Eurasia, and with berry fruit, and *Drypis*, with one species in south-east Europe, and with capsule with lid; but as these are small and rather local genera, and could evidently be split off from any genus with a capsule, it is unlikely that they were formed at this early stage. The next division in the key is more probably that which split off *Melandrium* with eighty species in the northern hemisphere, South Africa, and South America, which differs from *Silene* by its fully unilocular capsule as against a capsule multilocular at the base. In view of the great dispersal of *Melandrium*, it is by no means improbable that it may have been formed even earlier than *Dianthus*, and having met with greater vicissitudes, such as the separation of Old and New Worlds, has lost many more species than either *Silene* or *Dianthus*. In both *Melandrium* and *Silene* the capsule has two teeth to a carpel, and each has a closely related genus with one tooth per carpel, which was probably split off later (*Viscaria* near *Silene*, *Lychnis* near *Melandrium*). Further mutations might give the two genera *Uebelinia* and *Agrostemma* near to *Melandrium*, by changing the relative position of carpels and calyx segments, which are opposite in *Melandrium* and alternate in the two small genera—a change which could only come by some mutation. They might also give *Heliosperma* as a mutation from *Melandrium*, it having only two rows of papillae on the seed, instead of having them all over, and *Petrocoptis* as a mutation from *Lychnis*, the latter having the teeth of the carpel twice as many as the styles, the former once. It will be noticed that this phenomenon appears (in Silenoideae-Lychnideae) in two places, and must have appeared independently in these two, though the morphology or the structural features are the same in each case.

CHAPTER X

SOME TEST CASES BETWEEN THE RIVAL THEORIES

A. NUMERICAL

IT is now almost unquestioned that existing plants and animals have been produced by an evolution that, on the whole, has gone forward, producing organisms of increasing complexity such as man and the higher animals and plants. But many of the "lower" things, the seaweeds, the lichens, the smaller ferns, the insects, etc., have not been killed out, but have also increased very greatly in number. This has always been difficult to explain upon the current theory, but is perhaps more easy of explanation if we consider that evolution was not altogether a matter of continuous improvement in adaptation, at any rate as indicated in external characters, which are almost the only things to show us that there has been any great evolution at all.

We have seen that a good case can be made out for differentiation, in so far as it implies that a family most probably began (at one step) as one genus with one species, of family rank, giving rise later to other genera and species carrying the family characters (but often with modifications in various directions), and making in this way a family whose numbers would steadily increase, inasmuch as there was no *necessary* reason why any of them should die out, as there was under natural selection, which killed out the less well-adapted ancestors. The loss of this first species and genus would of course exterminate the family, but as it grew in size, the loss of one genus with one species would matter less and less, the rank of the genus with reference to the family becoming continually less, the smaller the genus in proportion to the size of the family.

The adoption of the theory of differentiation of course turns the working of the mechanism of evolution the other way round, and in the opinion of the writer puts events in their proper sequence. It therefore seems clear that the first thing to be done is to decide which of the two views is the more correct one to take. Did evolution go in the direction from variety and species towards higher forms (Darwinism), or in the reverse way (Differentiation)? Did the family begin as a species of family rank, or was it gradually formed by the destruction of intermediates?

We are still far from any understanding of the actual mechanism of evolution, but if we can feel sure of the direction in which it worked, we shall have made one step in advance which may open a way to profitable lines of research.

For example, take the case of economic botany, with its background of applied organic chemistry. So long as we imagine a plant A, producing a valuable substance *x*, to be descended from some ancestor unknown, and quite probably unknowable, we are heavily handicapped in tracing the origin and chemistry of *x*. But if the descent, as differentiation would have it, were the other way, and the actual ancestors of A may still be alive, so that their chemistry may be studied, the work is greatly simplified. Instead of remaining a vast mass of facts with little or no co-ordination, economic botany may become a definitely *scientific* subject, producing knowledge, not merely supplying it in a dictionary form, and we shall be able to look to valuable results as yet quite unforeseen.

Endemic or local plants, again, if they be regarded as usually the youngest in their own circles of affinity, and therefore as "the latest thing" in breeding, in chemistry, etc., may become of great importance, instead of being regarded as practically negligible relicts, as at present.

The writer hopes that the work here described may aid in putting workers upon the right path towards a discovery of the actual mechanism of evolution, and it seems to him that it may be to cytology that we should look for the next step in advance. As yet, the mutations that have appeared seem usually to be lethal, recessive, or non-viable, but this is no proof that viable or dominant mutations cannot appear also. If the result of such a mutation were to be found growing anywhere, people would at present say that it was another relic, and leave it at that. Guppy has pointed out that many of the species that have been found once only, and have never been seen again in spite of search, are quite probably the result of such mutations, which were in the early stages of establishing themselves, and were perhaps exterminated by collecting specimens, or were not viable (cf. 66, p. 151).

As the two theories of the direction of evolution are diametrically opposed, it seemed to the writer possible to devise some crucial tests between them. A number of these have been thought out from the principles laid down in *Age and Area*; these suggested others, which have led to more. This simple fact, that these principles can be so extensively used for prediction, goes to show

their general correctness, for the rival theory of natural selection cannot be used to make predictions at all. All the evidence obtained seems to point in the same direction, and seems to show that evolution is moving as an ordered whole, upon lines that have an arithmetical or mathematical basis. The general mathematical propositions that underlie the theory that is here being put forward have been worked out fully by Mr G. Udny Yule, whose paper (75) contains a very readable and simple general introduction and summary that should be read by all who take any interest in the subject under discussion.

The actual evolution of new genera and new species seems largely determined by a simple following, differing in speed in each individual case, of the law of continual doubling, as was shown by Yule and the author in 1922 (76). Sir James Jeans has said that "All the pictures which Science now draws of nature, and which alone seem capable of according with observational fact, are mathematical pictures." In this he was referring more especially to the physico-chemical sciences, but the work described here, and in *Age and Area*, gives the impression that biology will have to be added to them, though not in such a clearly-cut condition.

In this and the following chapters, some test cases are described, all giving evidence which seems not infrequently conclusive that the theory of differentiation, or divergent mutation, is a more probable explanation of evolution than is that of natural selection. The number of cases described may seem excessive to some, but the writer, who is now growing old, has tried to make his position as secure as possible, and has therefore chosen a number of tests from various parts of the subject.

TEST-CASE I. INCREASE IN NUMBER WITH EVOLUTION

It is admitted that as time has gone on, plants have increased vastly in number. But how did natural selection, working through gradual adaptation, produce such an increase? The very name selection would seem to imply the picking out of some from among many. One would expect the ultimate result to be a few "super-plants", not a vast and increasing number with no evidence to show that any one was superior to its immediate relatives.

On the theory of natural selection new variations, to have any chance of persistence, must have been produced so that accidentally or otherwise they suited the conditions, or more com-

monly, some difference in the conditions, better than did their immediate ancestor, which must have been suited to the conditions to survive and reproduce. This would most probably mean some difference in the physical conditions, especially of climate or of soil, or in physical differences due to the presence of other organisms, such as greater shade, greater demand for some chemical constituent of the soil, or other thing. But *why* should a change in soil, or in climate, or in biological surroundings, unless perhaps it were very strongly marked, involve any morphological change? It is very difficult to see any connection between these things.

Unless by some accidental happening, or in the rare case of a "pure stand"—a solitary species occupying a large area—the surroundings made by other plants would be continually variable. Weather also is changeable, and unless a species were suited from its birth to this fact, it would have a very poor chance of survival in any case. Soil varies from one spot to another, and so on. Unless variation in the conditions went continuously in the same direction, as for example in a change of climate (not of weather), it is very difficult to see why variations in the morphological characters of the plant should go always in the same direction, as is required if they are to be added up to make specific differences. And it is difficult to see why, for example, there should be any need for change at all in a species that occurs, as do most species, principally in one association of plants.

But to get increasing numbers of species, one species must (at any rate very often) give rise to two or more, not simply to one new one, unless, as on the theory of differentiation, the parent survive as well as the offspring. But upon the theory of gradual adaptation, to get two or more species from one without losing them by intercrossing in the early stages, one must have different conditions in different parts of the range of the same parent species. In other words, it must occupy a fairly large area to get into such variety, and this is the basis of the explanation of the local species as relics, though they far outnumber the widely distributed ones, even in the most "successful" genera.

But if all the local species are failures, where does the increase in number come from? Even in his own diagram (6, p. 90) Darwin begins with eleven species, which at the next stage become reduced to seven, the rest disappearing. At an indefinitely later stage, shown in faint lines, they have increased to

fourteen. The relative proportions of widely and of narrowly distributed species were not well known at that time, nor the relative proportions of the genera in a family, both shown in the hollow curves. Nor was it realised that no boundary could be fixed dividing endemic species or genera from non-endemic. A mere glance at the hollow curves will show this, or at a contour map (chap. XIII, case 27). Even the big genera consist largely or even principally of local or endemic species.

As an actual case, we may take the Monimiaceae, already described upon p. 33. There are two large genera and thirty small. What is selection going to do with these latter, which contain 30, 25, 15, 15, 11, 7, 6, 5, 4, 4, 4, 3, 3, 3, 2, 2, 2, 2, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, species respectively? The ones will presumably disappear first on the whole, and the family should logically be reduced ultimately to the two large genera of 107 and 75 species, most of which again are relics in the sense that they only occupy small areas. It is clear that natural selection, working upon the lines usually laid down for it, would result in a tremendous diminution. And not only do the numbers of species in the genera follow the law of Age and Area—the hollow curves—but so do the areas that they occupy. The diameters of areas occupied by genera of one or two species average about 560 miles, with three to five species about 830, with six to eleven 1766, with fifteen to thirty about 2310, and the two large genera about 5500 miles. One can draw no lines of distinction. If the ultimate end of natural selection is to be a small number, why begin with so large a one? Whence did they all come, and why were they evolved at all? Under differentiation expansion is the rule, for each one may ultimately give two, and there is no necessary reason for the older ones to die out as they must under natural selection. Once established in a small way, if there is no necessary difference in adaptational value between one morphological form and another nearly allied to it from which it may even have arisen, a species may go on indefinitely, though by reason of the presence of barriers to spread—physical, climatic, ecological, etc.—it may never be able to expand over very large areas of country.

The same results as are shown by the Monimiaceae are shown by any other family that one may take, especially if it be of fairly reasonable size. The Cruciferae, with 850 genera, begin higher up (with larger genera than the Monimiaceae) and end with 56 twos and 145 ones. The Compositae end with 148 twos and 446 ones (old figures).

It is difficult to understand, upon the theory of natural selection, how the long tails of genera that contain only one or very few species, and that occur in all but the very smallest families (and are often indicated there), ever came to be evolved at all. Natural selection looks upon them as the failures, and upon the large genera with many species as the successes; the latter are also widely distributed about the world in practically all cases. But *why* should a genus with many species occupy a large area? There must, upon the adaptation theory, have been in it a marvellous generic adaptation. If we take the first hundred genera in my *Dictionary* (5th ed.) with fifty or more species, half of them show a distribution right round the world, and at least half the remainder cover immense areas. The smallest ranges are those of *Acantholimon* (Eastern Mediterranean) and *Agathosma* and *Aloe* (South Africa). But, with ranges like this, these large genera must be very old, to have reached so many continents before communications were broken, and how did they come to find, in those early times, so great a variety of conditions as to lead to so many species, at a time when conditions are usually supposed to have been much more uniform than now?

If the small genera of one or a very few species are to be looked upon as relictus, why are there so many of them, and why do their numbers increase towards the bottom? It was shown (in 66, p. 185) that out of 12,571 genera of flowering plants, 4853, or 38·6 per cent, had only one species each, 12·9 per cent had two species, and 7·4 per cent had three. The numbers diminish upwards, following the regular hollow curve, shown not only by the grand total, but by each individual family down to quite small ones. The larger the family, the more accurately does it show the hollow curve, a fact which does not favour the view that the tail of small genera is composed of relictus. Why should a "successful" family have so many? One cannot draw a line through such a curve, and say that all on one side of it are to be looked upon as failures, on the other side as successes. To explain the curves, the selectionists are thus obliged to admit that natural selection shows its results in a continual and decreasing diminution of numbers, as indeed one would to some extent expect from its name. But if so, why did nature produce so many at first, only to cut them down later, and where does the increase in number come from, that is undoubtedly shown by the vegetable kingdom? Was there no selection in ancient times? Differentiation, on the other hand, as Yule has shown (75), necessarily results in

the production of genera in such a way that the result must be a hollow curve.

The result of this first test is thus clearly in favour of differentiation.

TEST-CASE II. THE SIZE OF THE LARGEST GENUS IN A FAMILY

On the theory of natural selection, the parent of a new species will tend to become a relic, ultimately disappearing, but on that of differentiation, there is no necessary reason why this should happen. The parent may survive, probably does, long after the throwing of offspring that may be specifically or even generically distinct. As time goes on, the mutations in any one line seem to tend to become perhaps less marked, so that generic mutations perhaps become less frequent in proportion. It is possible that at first, when considerable divergence is more easy, all or most of the divergences may be what we should consider as generic. But on the whole, it is evident that in any case the earlier members of a family should be larger than the later ones—in numbers of species if genera, in area occupied if species. They started first, and on the average they should keep in front, so long as one considers only related forms growing in similar conditions, as already fully explained in *Age and Area*. The oldest genus in a family, therefore, should in general tend to be the largest genus in it, and the older and larger the family, the larger should its largest genus be. But we have no absolute test of age, and must not try to make comparisons of age, except between close relatives in similar conditions. To say that the largest genus in a quickly reproducing, mainly herbaceous family like the Compositae is older than, or even as old as, the (far smaller) largest genus in the slowly growing and reproducing giant trees of the Dipterocarpaceae, is to make a statement which has nothing whatever to back it. The latter, though only 5 per cent of the size of the first, may even be very much the older genus. All kinds of accidents also interfere with arithmetical regularity in these matters, so that it is really very astonishing to see how regular the figures are, in spite of all the geological or climatic changes, or other outside interferences.

None the less, as has already been shown in *Age and Area*, p. 188, the supposition that the size of the largest genus goes with the size of the family (a fact which *could* not be predicted by the aid of natural selection) is borne out when one takes averages.

The table given there shows this clearly, and some later figures show it equally well:

Size of family in genera (not in species)	Average of the largest genera in each (species)
1	12
2-3	43
4-8	94
9-20	129
21-40	153
41-70	195
71-100	313
101-250	330
Over	611

The requirement of differentiation, that the size of the largest genus of the family shall go up with that of the family itself, is fully borne out, while no theory of natural selection or of gradual adaptation can offer *any* explanation of the facts.

TEST-CASE III. THE RELATIVE SIZES OF GENERA

We may now consider the relative sizes of the genera in a family or other group. Upon the theory that they were formed by gradual adaptation one cannot say more about their probable relative sizes than that some (the "successful" ones) will probably be large, and some (the "failures" or "relics") small. Nor can one give even an indication of what their relative numbers will be. Further, one will also be inclined to expect to find some kind of distinction shown between the successes and the failures. But if differentiation be the more correct view to take, evolution is no longer of necessity a *direct* expression of continually improving adaptation, nor is the geographical distribution of plants. It is clear that if that be so, there would be little reason for one plant to spread, on the average, faster than its near relatives. All in a related group would tend to spread at a more or less uniform speed. But the speed of spread would depend upon many factors, and to average these out, as already explained in *Age and Area*, plants should only be taken in groups of say ten allied forms, which should only be compared with other tens allied to the first. Plants of systematic affinities that were widely different might spread at completely different speeds, or plants that differed in habit, like trees and herbs, or in speed of reproduction or other things. But on averages, with groups of allies growing in fairly similar conditions, the oldest genus of a family should be the largest, whilst the others should show a continually

decreasing size, but increasing numbers, with decreasing age. The result would be to give one of the hollow curves which we have described above. A little thought will soon show that the diminution in size will not be proportionate to that in age, for the older that a genus is the more rapidly will it tend to gain upon those younger than itself (66, p. 34).

As a genus or species (they are the same at the start) increases in number of individuals and in area occupied, it will begin to "throw" offspring differing from itself, by mutations occurring at infrequent intervals, sometimes of generic rank, but more often of specific. The average size of a genus is about fourteen to fifteen species, but this does not mean, as one is tempted to suppose, that a generic mutation may occur once in fourteen to fifteen times. Rather it means that the average age of a genus may be more or less represented by the average age of those which possess fourteen to fifteen species. Some of the throws will be undoubted species, some undoubted genera, some again of doubtful rank.

Supposing, which seems the most probable, that a new species or genus begins upon a small area, it will probably be a very long time before it occupies a more considerable space with more individual representatives. But while it may wait a very long time for the first throw, it would seem probable that the frequency of the throws will on the whole increase with the number of the individuals in the species, which in turn will tend to increase more and more rapidly as time goes on (cf. *Age and Area*, pp. 33-4). The first line of descent, that from the original genus (and species, of course) of the family, will always have the start of the second, which arises from the first generic throw of the original genus. But as time goes on, there will be a continually increasing number of lines of descent with the continual formation of more and more genera to head them, so that at last we shall get the familiar curve shown by any table of numbers of species in the genera of any particular family of reasonable size. Thus a recent enumeration of the Caryophyllaceae (35) gives the following figures (bigger genera obviously rounded to nearest ten or more):

400, 300, 160, 100, 100, 90, 70, 40, 40, 30, 30, 30, 25, 23, 20,
20, 20, 20, 18, 16, 15, 12, 10, 10, 10, 8, 7, 6, 6, 6, 5, 5, 5,
5, 4, 4, 4, 4, 4, 3, 3, 2, 2, 2, 2, 2, 2, 1, 1, 1, 1, 1, 1, 1, 1, 1,
1, 1.

If, then, genera are formed upon this principle—and that this is quite a probable approximation to what really happens is

shown by the universality of the hollow curve—we shall expect to find that there will be a *gap* between the numbers of species in the two largest genera of the family. This gap will obviously be due to the fact that the two first genera of a family will usually have been formed the one a good while before the other. During that interval of time the first one will probably be able upon the average to throw one or more species before the second genus appears. It will thus get the start of the latter, and will continually gain upon it. It follows from this that the larger the original genus *now* is, the greater, on the average, should be the gap between it and the second genus. As we have just seen, the third genus of a family will, upon the average, be separated from the second by less time than is the second from the first, and the time-separations will become less and less as we go downward to the smaller genera. We shall, therefore, expect the gaps in numbers of species also to lessen.

Turning to the facts, this is exactly what we do find. Out of all the families given in my *Dictionary*—about 240 with two or more genera—only eleven, mostly very small, show no difference between first and second genus. The two larger families are Bignoniaceae and Sapotaceae, where the four top genera are all given as having 100 species. But on the average of all the families, the first difference is ninety-nine, while the second gap is only thirty-two, the third eleven, the fourth eleven, the fifth six.

The result of this test case, therefore, is in favour of differentiation. In fact, one cannot, with progressive arithmetical links like these between the genera, consider natural selection or gradual adaptation as having had much to do with the evolution.

TEST-CASE IV. PROPORTIONS OF SMALL GENERA IN FAMILIES

If natural selection of gradual adaptation be the moving power of evolution, and the small genera and local species be the relics of what must be regarded as the failures, then one would certainly expect that these ought to be more numerous in proportion in the small and local families, which are also regarded as relics. If, on the other hand, differentiation has been the mechanism, one will expect that the larger a family grows, the more rapid will be its proportionate production of small genera, for each genus, whether small or large, may be able to throw new ones, so that the small genera will be increasing (in number, not in size) more rapidly than the large, the family following the hollow curve.

If we test these suppositions upon the facts, we soon find that the large and "successful" families have many more "relics" in them than have the small and "unsuccessful". In the Compositae, the largest of all, the monotypic or one-specied genera form 37.8 per cent of the total, while in the 151 small families containing not more than ten genera each they are only 29 per cent (figures twenty years old). The families with eleven to fifty genera have 38 per cent of monotypes, those with fifty-one to one hundred have 36 per cent and those above have 39 per cent, a result which agrees well with the theory of differentiation, but not with that of natural selection. Even with the ditypic genera, their percentage in families up to 200 is 12.25, and 12.75 above.

If the small genera of one or two species are to be looked upon as relics of former floras, why are they so numerous? About 38 per cent of all genera are monotypic, and over 12 per cent ditypic, so that these groups alone make up half the total number. Over 80 per cent of all genera have ten or fewer species. The hollow curve, as we have seen, goes so smoothly and uniformly that there is no possibility of drawing a line between successes and failures. The only explanation of these curves upon the theory of natural selection would seem to be that selection, as indeed one might expect from its name, is continually picking out fewer and fewer, so that its effect will be ultimately shown (when the relics have died completely out) in a vast *diminution* of the numbers of species and genera. In other words, it is on its way to pick out a few "super-plants" from among a mass of inferiors. But if so, why did nature begin with so many? Their evolution cannot be explained by natural selection. The whole attempt to explain things upon this theory leads to so many absurdities that it becomes untenable. The simplest explanation is evidently that by using the theory of gradual adaptation in structural characters one is trying to work *backwards*.

Every formation of a genus of two species (perhaps one may be enough) increases the number of genera that may be looked upon as capable of giving new genera of one, and as the larger genera also may be looked upon as similarly capable, the rate of production of monospecific genera will increase with the size of the family. As already explained, the ones, as newcomers, will be particularly slow at first in establishing themselves, so that there will always be a time lag between them and the twos.

This test also fully favours the theory of differentiation.

TEST-CASE V. THE HOLLOW CURVE

Many years ago it was shown that this curve, which is described in *Age and Area*, p. 195, and in Chap. IV above, is a universal feature of distribution in plants and in animals, both in regard to the areas occupied, and to the sizes of the genera in families by number of species contained. When plotted logarithmically, in the latter case, they give close approximations to straight lines, showing that they have the same mathematical form, and must be due to the operation of the same law. The production of such curves seems to the writer to place an almost insuperable obstacle in the path of those who would explain evolution and distribution in terms of gradual adaptation by means of natural selection. Yule has shown (75) that the curve would result from the continual doubling of the species and genera concerned, when one supposes the parent to survive as well as the offspring, as is the case according to the theory of differentiation. The curve then becomes a normal and *necessary* feature of the evolution that is going on, whereas under the theory of natural selection it is totally inexplicable. Opponents have tried to belittle it by showing that one can get similar curves from the names in the telephone book, and such like conglomerations of inanimate things. I have lately shown that the distribution of family surnames of farmers in Canton Vaud (69) is just like the distribution of species, and therefore must follow the same laws, as it gives the same curve. Natural selection *could* not determine it, therefore it cannot be the determinant in the general distribution of plants.

Nothing but a uniform pressure would ensure that results could be expressed in hollow curves. Family by family, and genus by genus, whether in numbers or in areas, all alike obey the same law. Natural selection could not produce results like this, and the only cause yet suggested is age, which represents the resultant of all the forces acting. If they produce an average result of x in a long time 1, they will produce $2x$ in time 2. Age thus forms a measure of distribution, but one cannot compare, unrelated forms, and must always work in tens of allied species, to average out the differences that there may be between them.

It is clear that this test gives an unqualified verdict in favour of differentiation.

TEST-CASE VI. SIZE AND SPACE

The hypothesis of Size and Space is more fully described in *Age and Area*, p. 118; it follows from that hypothesis. "On the whole, keeping to the same circle of affinity, the larger families and genera will be the older, and will therefore occupy the most space." If adaptational improvement ceases to be the prime (or even perhaps an important) factor in evolution, there is no special reason why one species should spread more rapidly, or over a greater area, than other species *closely related to it*. As an illustration the case of distribution of species in Britain was taken, and it was shown that it increased with the size of the genus.

"A good proof for the general correctness of Size and Space is that...the further out we go among the islands, the larger on the average do the genera become (in the number of species that they contain in the world). Whilst the world average for a genus is 12-18 species, the non-endemic genera found in India contain on the average about 50 species in the world, in New Zealand about 75, and in the Hawaiian Islands about 100.

"The smaller families usually occupy smaller areas than the larger, and the question arises whether they should be considered of equal rank to the latter. Guppy has suggested a grouping of families into classes based upon these principles, for which he has suggested the title Rank and Range, and it is clear that in all future systematic work, the question of area must occupy some attention" (66).

It is clear that the facts shown under Size and Space cannot be explained by aid of the hypothesis of natural selection or of gradual adaptation, and can at present only be easily explained by that of differentiation.

**TEST-CASE VII. "SOME STATISTICS OF EVOLUTION
AND GEOGRAPHICAL DISTRIBUTION,
AND THEIR SIGNIFICANCE"**

To give details would simply be to repeat the paper of Mr G. Udny Yule and the author, in *Nature*, vol. cix, 9 February 1922, p. 177, and it will suffice to call attention to it. The general conclusion was that: "Inasmuch as all families, both of plants and animals, show the same type of curve, whether graphic or logarithmic, it would appear that in general the manner in which evolution has unfolded itself has been relatively little affected by the various vital and other factors, these only causing deviations this way and that from the dominant plan." It follows that evolution must have been by mutation, and that this must, at times anyway, have been large, as demanded by the theory of differentiation.

**TEST-CASE VIII. THE HALVING OF THE
SPECIES IN A FAMILY**

We have seen (p. 96) that, in general, there is one genus in each family which on the average has at the present time nearly a hundred species more than the second genus; the difference is only on the average thirty-two between the latter and the third genus, and so on. Only when one comes down into the smaller genera does coincidence in number happen at all seriously, and it happens more and more the nearer one comes to the bottom of the list, so that at last, if of any size, the family ends with a streamer of monotypic genera, or genera of one species each. This hollow curve, which is always formed, is what is to be expected upon the theory of differentiation, and natural selection is helpless to explain it.

The hollow curve is due to the continual doubling of each genus in turn by the throwing of a new genus so that, as time goes on, the total number of genera undergoes an increase, which is continually more and more rapid, as the numbers grow. And as time goes on, the genera already formed are supposed to increase their number of species in the same way. We have supposed, as the simplest solution of the problem for the meanwhile, that each genus will on the average throw a new genus rather than a new species once in every so many throws. In the counting that is being used for this particular paragraph,¹ the total number of families with more than one genus is 285. Taking the number of species in each genus of a family, and arranging the genera in descending order, the total number of species has been counted for each family, and halved, and a dividing line drawn immediately to the right of the genera required to make up the full half. This of course means that the genera on the left may contain the exact half (this is rare) or slightly or even considerably more; but the numbers on the right-hand side of the line never exceed, and very rarely equal, those on the left. For example, three families are given:

Aristolochiaceae	800	60	10	8	1	1	1
Basellaceae	14	3	1	1	1		
Elatinaceae	19	19					

All of these have the dividing line after the first genus, and this proves to be the rule when the family is small, but not when it is large. Out of the 285 families, no fewer than ninety-eight, or 41.7 per cent, have the dividing line after the first genus, as shown

¹ The numbers are continually being revised for my *Dictionary*.

above. Fifty of them have two, three, or four genera, the actual figures for the whole number being 22/2 (twenty-two of two genera), 21/3, 7/4, 9/5, 8/6, 6/7, 2/8, 5/9, 2/10, 2/11, 1/12, 1/13, 2/15, 2/17, 1/19, 2/21, and one each of 24, 26, 28, 78 (Moraceae) and ninety-nine genera (Solanaceae). Arranging these ninety-eight families in order of size of the largest genus in each, one finds that though the average size of the families in each group of ten goes down with the average size of the largest genus, there are nevertheless, in the first ten, four families with less than ten genera each, but each headed by a very large genus (*Begonia*, *Oxalis*, *Piper*, *Impatiens*).

The next lot of families is composed of those where the dividing line comes after the second genus, as in Primulaceae: 250, 120, 90, and so on to ten ones, total 651. While the average size of the ninety-eight families with dividing line after the first genus was 7.9 genera with 201 species, the average size of those with the line after the second genus is 14.9 genera with 249 species. Going on in the same way through the whole number, we get the following table:

Dividing line after the	Families	Average	
		Gen.	Spp.
First genus	98	7.9	201
Second	50	14.9	249
Third	22	31.6	571
Fourth	20	63	997
Fifth	10	72.9	847
Sixth	6	73.2	1036
Seventh to tenth	18	128	1486
Over	16	387	5050

Figures in italics break the regularity of the table of averages.

The larger, on the average, that the family becomes, the more is the dividing line pushed to the right, until in the Compositae, the largest family of all, it only appears after the thirtieth genus.

It is clear that there is some arithmetical reason behind all this, and the simplest explanation is that it is due to the continual increase of species in genera other than the original one, when the latter divides off new genera (which again divide) at average intervals. In any case, the facts do not agree with any hypothesis of gradual adaptation working from below upwards.

These numerical tests, to which others might be added, are thus all in favour of differentiation rather than of natural selection or of gradual adaptation.

CHAPTER XI

SOME TEST CASES BETWEEN THE RIVAL THEORIES

B. MORPHOLOGICAL

NATURAL selection, being a common phenomenon of everyday experience, has exercised such a fascination that it has to a notable extent inhibited people from trying properly to think out how a principle, whose essence is competition with partial escapes into usually temporary success every now and then by improved adaptation, can produce the ordered arrangement, taxonomy, and morphological or structural uniformity with which we are familiar. Herschel the astronomer, in an early criticism of the *Origin of Species*, is said to have called it the "law of higgledy-piggledy", and when one tries to imagine what morphology would be, under its unrestricted operation, it is difficult to meet this criticism. Why should natural selection produce such comparative uniformity in morphological structure? Why should there be such morphological likeness between the members of whole families, tribes, genera, or even divisions like the Monocotyledons? Why should the morphology remain the same, and not improve in later evolutions? Why should the larger (older) families appear in almost every kind of ecological conditions, though the members of any one of these families show greater structural resemblance among themselves than do the plants of the association that inhabits any given spot? A grass is an unmistakable grass, whether in the tropics or in the arctic zone, in a dry or in a wet climate, in a bog or on a moor. To say that this is the case because it is a grass, and must retain the morphology of a grass, is no explanation, but only throws the task of explanation a little further back. *Why* and *how* were the grasses, or the crucifers, or the composites, evolved at all? Why is there nothing in common, in structural features, between say a grass and a crucifer growing in the same kind of conditions, and side by side, on a moor or in a pasture? One would expect natural selection, working by gradual adaptation to similar conditions, and determining the structural features (as it *must* do if it is to be an explanation of evolution) to produce something of similarity. In

actual fact, however, there is rarely much or any structural likeness among the members of a given association of plants, unless they happen to belong to the extremes of the principal ecological divisions like xerophytes on the one side and hydrophytes on the other, or to special ecological groups like climbers or parasites, which do not, incidentally, grow in any special conditions, or in associations. Even in these cases, the ecological characters that mark them are rarely such as have great importance in classification.

Were it not for the great structural differences that exist, we could not tell that evolution had gone on to so great and complex a degree. There might be herbs, shrubs, and trees, water-plants, epiphytes, climbers, plants of dry climates, bulbs, tubers, and so on, with other more or less adaptive forms, but there seems no *a priori* reason to suppose that we should find such things produced by an adaptive evolution as the structural differences that mark whole families like the grasses or crucifers, and distinguish them from one another. As Went has said (50), we see the morphological differences, and assume that they must have some physiological explanation. But there is nothing to show that there is any physiological need for them. What connection can be shown between the great bulk of the structural features of plants and their physiological necessities? Man is adapted, region by region, to almost every kind of conditions that can be found upon the surface of the earth, yet he is all undoubtedly of one species, and does not show any great structural differences. And there are numerous similar cases with plants, though these are slower in movement, and have not covered so much ground. Some cover a very large area with no serious structural differences, like *Hydrocotyle asiatica*, *Sanicula europea* or *Hippuris vulgaris*, while in other places where the conditions are very much alike throughout, a genus may show a number of species. One can rarely infer from the external features of a plant, e.g. in a herbarium specimen, or even in a living one, from what kind of conditions it came. In the vast majority of cases, the most minute morphological description will convey nothing as to the habitat or the physiology, unless the plant happens to belong to one of the great ecological groups like water-plants or climbers. Can anyone read the characters in the most minutely descriptive flora, and locate the probable types of habitat of the plants?

Taking genera with more than one species in the British flora, the first, *Thalictrum*, the meadow-rue, has three. *T. alpinum*,

with a bi-ternate leaf, grows in alpine bogs, *T. minus*, with a tri-pinnate leaf, in chalky pastures, and *T. flavum*, with a bi-pinnate leaf, on river banks. In the next genus, *Anemone*, *A. pulsatilla*, with a bi-pinnate leaf, grows in chalky places, and *A. nemorosa*, with a ternate leaf, in woods. Yet these two genera are closely related, and surely, if the structural forms of the leaves had *anything* to do with the conditions, the two with the bi-pinnate leaves would occupy places not very dissimilar. The usual reply of the selectionists to questions like this, that at some time there must have been such conditional differences that a difference like that between these various types of leaf had a physiological significance, is simply an appeal to ignorance, for which there is not the slightest evidence.

If one takes the matter the other way round, one gets a good argument against this contention of theirs. Why does one find pinnate leaves, to take just a few examples from the British flora, in *Clematis*, climbing in hedges, in *Nasturtium* in wet places, in *Cardamine* in meadows, *Anthyllis* in dry pastures, *Vicia* climbing in waste places, *Spiraea* on downs, *Potentilla* by the roadside, *Rosa* in hedges, *Myriophyllum* in water, and so on; and why in *Geum urbanum* are the pinnate leaves only the lower, radical, leaves of the plant? The argument of the selectionists is clearly an admission of the point for which I am contending, that adaptation is mainly an internal, physiological, or functional process, without any necessary influence upon the outer, structural features of the plants concerned.

The Englishman is successful enough in the conditions that obtain in England, but if taken directly to India, and asked to make good in the conditions to which the natives of that country are subject, he would fail, primarily on account of the very different climate. But he might succeed, if he were adapted by nature's method of extremely slow change, say in a quarter or half a million years. But by quick change he would be like the potato and the dahlia, which have not yet become acclimatised to Europe. Time is the needful thing in acclimatisation and adaptation, and nature has plenty of it available. But it is of course by no means unlikely that so great a change would be beyond the limits of the Englishman's possible adaptation; there are many cases in plants which seem to point to the existence of such a limit. From what we know of man, it is not to be expected that in the course of this adaptation the Englishman would suffer great morphological changes, though he might acquire a darker

skin, as apparently have other northern tribes that migrated into India. The principal change that he would undergo would be a gradual physiological adaptation to warmer climates.

Many, if not most or even all, of the characters of distinction that mark families, sub-families, and even smaller groups, are such that they can have no serious value upon the physiological side, which is the only one that matters from the point of view of natural selection or gradual adaptation. Only upon things with functional value or disadvantage can natural selection operate, and, as has frequently been pointed out by the writer and others, its important work seems to be the killing out, probably rapidly, of any variation definitely disadvantageous, though even here, as the struggle for life is mainly among seedlings, disadvantageous characters that only appear late in life may quite well survive. There is no doubt that natural selection would encourage the success of a new and improved form that had just arisen, but there is no evidence that it can *continue* to call up small variations or mutations always in the right direction, or that it can pass the rough and ready line of distinction that exists between species, that of mutual sterility, unless some mutation should happen that will do so. But work of this kind will not ensure progress such as seems to be the mark of evolution in general. Suppose a whole family to possess a septicidal capsule, or diplostemonous stamens. There is no evidence to show that there is any physiological value attaching to this possession, which in any case only appears in later life. One cannot imagine natural selection killing out a member of the family that had adopted (or was varying—if it could so vary—in the direction to adopt) a loculicidal capsule, or obdiplostemonous stamens, or was even going so far as a septifragal capsule. The family constancy of the capsule or the stamens must be due to inheritance from a common ancestor. But how, under selection, did the ancestor of one family obtain one kind of capsule or stamens, of another family another? With the recent revival of natural selection, there has been a recrudescence of the idea that characters that are of no physiological value tend to be very variable, but if so, why are family characters less variable than generic and specific, though they are admittedly of less physiological value?

Plants, animals, and man alike tend to produce so many offspring that, in a short time, but for various unfavourable conditions, there would not be room for them upon the surface of the earth. The illustration taken from the rapid multiplication of the

green-fly is well known (42, p. 188) and even in the Podostemaceae, annuals starting again every year, one plant might in four years cover about 100,000 square miles. The fiercest struggle for existence comes to a plant at birth, and any that is not suited to the conditions as they are *at that moment* will be killed out by natural selection by reason of unsuitability, though of course mere chance will have a large influence in the matter. But this is an individual struggle, and we have no right therefore to assume that species struggle *as units*. Nothing can come into permanent existence without the permission of natural selection, but once the newcomer has become established in a few places reasonably far apart, the chance of its being completely killed out will steadily diminish, and in course of time may be reduced to vanishing point. Natural selection simply determines in each individual case whether or not a given plant shall be allowed to survive and reproduce.

Very few indeed of the morphological features that distinguish one organism from another that is related to it have any physiological significance at all, especially in those features that separate the higher groups of plants from one another. Even the bulk of the generic and specific characters come into the same category. One cannot imagine any adaptational reason why *Ranunculus* should have over 300 species, and world-wide distribution, while its closest allies, like *Myosurus* or *Oxygraphis*, have few species, are comparatively localised, and differ largely in the fact that the wall of the fruit is not so hard. Still less can one imagine adaptational reasons taking part in the separation of the family Ranunculaceae into a group with achenes and another with follicles, or one with alternate leaves and one with opposite. Nor can one suggest adaptational reasons for the existence of 200 species of *Clematis*, and still less for that of a couple of thousand *Senecios* or *Astragali*. If natural selection is to be held responsible for the vast dispersal of, and numbers of species in these genera, they must have some very great adaptational advantage over their close allies. And the adaptation which was so successful must have been *generic*, for most of the species have but small areas. There is no species in these very large and widespread genera whose range covers that of the genus, though in smaller and less widely dispersed genera this is very commonly the case.

It has frequently been shown, e.g. by de Vries (66, p. 224) and by J. T. Cunningham and others, that adaptation shows chiefly

in generic and family groups, rather than in specific, so that any theory that tries to explain it on the basis of a commencement with the species, as does the Darwinian, *must* fail in its explanation. What adaptation there is, is rather handed *down* by heredity.

The things that are usually considered to be gradual adaptations are steadily diminishing in number (cf. p. 116), and though it may come as a shock to some, one must add such things as climbers, parasites, saprophytes, lichens, fungi, herbs, trees and so on, for in most of these cases no intermediates are possible, or at any rate probable, and so much correlation (p. 129) is also required, which could not be effected by gradual adaptation. Trees, for example, are usually supposed to be older than herbs, but can any one imagine them being gradually selected down to herbs, especially when one remembers that both forms may not infrequently appear in the same genus, so that it is evidently, as in so many other cases, quite a simple matter to pass from one to the other?

One might ask similar questions for the whole list of characters of family rank (Appendix I). Is there any adaptational difference between a superior and an inferior ovary, any between parietal and axile placentation, trimerous and pentamerous flowers, a dorsal raphe and a ventral, one cotyledon and two, or the various kinds of zygomorphism? Incidentally, median zygomorphism is looked upon as an adaptation to the visits of insects, but if so, why do transverse and oblique zygomorphism exist also? Why do the highly zygomorphic flowers of the Podostemaceae stand stiffly erect, whilst they are wind-pollinated also?

Or, to go to generic characters, and taking a small family like Styracaceae, is there any adaptational difference between a flower with ten stamens and one with five? Between an ovary 3-locular below and unilocular above, and an ovary 3-locular throughout? A flower with connate petals and one with free? Or, in the Caryophyllaceae, between a glabrous and a hairy stigma, a petal claw with and without wings, a capsule with teeth as many as carpels and one with teeth twice as many? We may even go on to species and still fail to find adaptational characters. It is impossible to read into the distinguishing characters any adaptational meaning which would be of any advantage in the struggle for existence, especially when we remember that the great struggle comes before the great bulk of these characters appear at all. It is an axiom in taxonomy that the less that any character

has to do with the life of the plant, the more important is it from a taxonomic point of view. The higher one goes from species to family, the less connection have the characters with the life, and if one tries to think out how a mechanism like natural selection, depending upon improved adaptation, could thus have less and less to do with adaptation, the more it separated into larger groups the organisms with which it was concerned, one will speedily arrive at a deadlock.

Two species usually differ in more than one character, even when closely related, and among the supporters of natural selection it is, or has been, very often an implied assumption that a species A shall change fully to B before it goes on to become C. But one can see no reason why this should be so; a variation in the direction of C would probably be just as useful in a plant that was only on the way to B. Natural selection can do nothing till the right variation is offered to it. Let us suppose that A is offered a variation in the direction of B and has started to adopt it, and that then a new variation is offered in the direction of C, obviously better, but in a different direction. What will happen then? Will it go on towards B and ignore the later offer, will it form C with a shade of B about it, or will it try to go back, and get rid of the traces of B, with the risk that it may not get another offer of C? There seems almost nothing for it but to demand that variations shall not interfere with one another, but that the one "in possession" shall be allowed to finish what it began, before another one is allowed to start. But this will greatly slow down the process of evolution, unless the variations are largely correlated. But why under natural selection should there be so much correlation? It is hard enough to find adaptational reasons for one variation, let alone half a dozen correlated ones. It would seem more probable and reasonable that in general the morphological characters have no necessary physiological value, and are therefore not the result of any adaptational selection. If a new structural character appears that has an adaptational value, it is at once seized upon and perpetuated, unless in case of evil chance. But to regard structural characters as necessarily showing individual adaptational value—for example, that there is some necessary value in a pinnate rather than a palmate leaf, or vice versa—is to stretch the theory of gradual adaptation too far.

It is a very remarkable thing that we do not find plants with a superposition of variations, one complete, the other incomplete.

The only reply the selectionist can make is to say that the constitution of the plant does not allow of the mixture of characters, or, in other words, that structural considerations override adaptational. And as this reply comes in, in nearly all cases, it does not leave much room, if any, for gradual adaptation.

The whole subject has suffered from the lack of proper thinking out. Everyone can see the struggle for existence going on before him at any moment. The *individual* who is in any way handicapped, be it by some physical disability, by poor health, by low intelligence, by parental poverty (resulting in cheap schooling, underfeeding, etc.), or by other difficulties, is *on the whole* the one to be defeated. In the early days of the theories of Malthus and of Darwin (which was based upon Malthus) the tendency was to legislate (or rather not to legislate) in such a way as to leave the struggle for existence uncurbed, the idea being that in this way the best was brought to the top and the inferior left at the bottom, if not killed out. The theory of "nature red in tooth and claw" had, and still has, a great vogue. It was not realised that the winners in the struggle for existence owed their success only too often to some adventitious advantage which was not necessarily part of their own equipment. Money, for example, providing the best food and education, was a great help. One has only to examine the trend of modern social legislation to see how we are drifting away from the old philosophy of the unrestricted struggle for existence. Everything possible is now being done to remove the handicaps that formerly were fatal to some of the best men, and to give to everyone the best possible chance, and there is reason to hope that in a few generations the results of this work will show a great social advance.

Man is all of one species, and it is worthy of note that in his struggle for existence against members of *other* species, he has owed his success not to the slight morphological differences that distinguish his different varieties, but to internal adaptation of brain, etc., leading to greater skill in handling the difficulties that beset him.

TEST-CASE IX. DIFFERENCES IN GENERIC RANK

This test will be rendered more intelligible by aid of the figure (8), in which *A* represents a family of two genera only, *B* a family of intermediate size, and *C* a large family, both *B* and *C* being imagined a good deal larger than here shown. All are supposed accepted by the same systematists, to make their rank fairly

equal. The diagram will serve for the growth of the families under differentiation, in which progress is supposed to work downwards from the original species and genus that began the family, *A*, *B*, or *C*, both species and genus of course being the same plant. As the family grows, it will form new species and genera, and *all* will on the average survive, so that the now existing family is in each case represented by all the dots under *A*, *B*, or *C*. Whether the whole family, if seriously old, survive like this, will depend upon

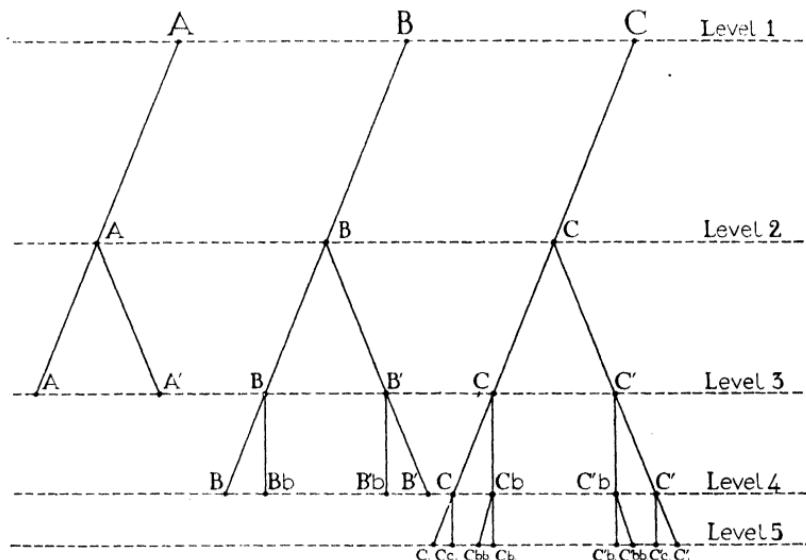


Fig. 8. Diagrammatic origin of small, medium and large families under differentiation, to show relative rank of genera in each, which goes more or less with the line 1, 2, 3 etc. upon which they happen to stand.

what geological or other catastrophes it has met with, and whether any *general* change may occur in a genus, causing its death, or transforming it, or more probably one of its species, into another genus. The well-known fact that the smell was lost at the same time by all known examples of the common musk, once universal in cottage windows by reason of its sweet scent, shows that though a species may be represented by innumerable individuals, something may happen simultaneously in the internal make-up of all of them. And there is nothing to show that larger mutations than this are not possible. The way in which the successive fossil species of *Stratiotes* appear in different geological horizons, each specifically different from the preceding one, shows the kind of

thing that may possibly happen, and again we have no reason why the change should not sometimes be generic as well as specific (8).

Under the theory of natural selection, the existing plants will only be the lowest row in each family, for evolution, as we have already explained, is at present supposed to work by the formation of slight varieties, which gradually increase to larger, to species, and so on, by the killing out of the less well adapted ancestors, while the ultimate survivors in the way of genera tend to be those that show the greater divergences. And the smaller the family, the greater are the divergences between its genera.

To return to the diagram, under the supposition of evolution by natural selection, the various genera that occupy the bottom row in each family, whether in line 3, 4 or 5, will simply be genera, or generic stages in the evolution that is continually going on. Under this supposition, there is no reason why the genera in the lowest line, 3, of family *A* should in any particular way be any different from those in line 4, of family *B*, or these from those in line 5, of family *C*. Nor does natural selection offer any test by whose application we may gain any idea as to the relative degree of divergence that there may be between the genera of *A*, *B*, and *C*. But upon the theory of differentiation or divergent mutation we shall expect that *the divergence between the two genera in family A will be about equal to the first divergence in the families B and C, i.e. equal to the divergence between their tribes or sub-families*. At the same level in the diagram, in other words, there will be more or less equal divergences. It has long been known as an axiom in taxonomy that genera in a small family are much better separated than genera in a large one, and here is a simple explanation of this. As the family grows in size, new mutations will come in at more and more frequent intervals, but within, or close to, the original divergent mutation. In other words, all the family, sprung from the original genus and its first mutation, will show some at least of the characters shown by these first two genera, which by the hypothesis of divergent mutation will tend to be very divergent. The original family characters will show best in the largest genera, which will be the oldest in the families, and carry the most of the earliest characters. The genera sprung from later mutations will not have, so well marked, many of the characters of the earlier mutations. The generic characters will necessarily become on the whole closer and closer together as the mutations to which they are due are less and less far back in their

ancestry. It would also seem as if there were a tendency in each family for mutation to become less pronounced as time goes on, so that the appearance of what we usually call family characters (list in Appendix I) becomes less frequent in proportion to the total of characters that appear. On the whole, there is more room for wider divergences the nearer one is to the starting-point of the family, i.e. to the original genus which gave rise to it, upon the theory of differentiation. Upon that of natural selection, it has always been a great difficulty to explain why the divergences became greater the higher one went in the key from species upwards. Why should natural selection cause the disappearance of just those forms necessary to make the divergence increase? This is inexplicable by natural selection, working upwards from small differences, but simple to differentiation, working the other way.

This being the expectation, we have only to look at Appendix III which gives the distinguishing characters of the two genera in those families that contain two only, to see that the facts agree with what was expected. The divergences are obviously of the same rank as those given in Appendix I as being "family" characters. If, on the other hand, one compare the generic characters in larger and larger families, one finds that as one goes up the scale, the genera, as one will expect under the theory of divergent mutation, get closer and closer together as new ones are "squeezed in" among the old. In a really big family, like the Umbelliferae, Compositae, or Gramineae, it is a familiar experience that it is as difficult to make out the genus, as in a small family to make out the species.

It is clear that we have not properly taken into consideration the *relative rank* of genera and other groups. In a very large family, where the genera have become closer and closer together by the continual appearance of new ones, the generic rank is evidently lower than it is in a normal small family. The ranks of all divisions in the classification, whether tribes, families, or genera, depend to a very great extent upon their relative sizes in their circles of relationship. This conception of relative rank has gone neglected during the reign of natural selection, to which a genus is simply a generic stage upon the upward road.

If, on the other hand, the small family is to be regarded as a relic, as is done by the supporters of selection, it becomes necessary for them to explain why the divergences of the two or three genera that are left is so great, and equal to the divergence of the sub-families in a large family. Often one hears people say that

the sharpness of definition in a small family is *due* to the fact that the family is small, with few genera. But this does not explain the fact that those genera have almost without exception the rank of sub-families in a large family.

The result of this test case is thus very strongly indeed in favour of the theory of differentiation as against that of natural selection with gradual adaptation.

TEST CASE X. THE PERFECTION OF CHARACTERS

The fact, which seems to have been completely ignored, that structural characters are practically always shown both by animals and by plants in their perfect condition, is one which is simply incapable of explanation upon the ground of gradual acquirement, but simple if it be the result of a sudden mutation. The astonishing thing in the latter case would be to see an imperfect acquisition. The perfect condition is best shown by the very widely divergent characters, like opposite or alternate leaves and many others that have no intermediates, in fact most of the characters shown in Appendix I. How can the divergence, under natural selection, have become not only larger but more perfectly marked? Supposing for the moment that an intermediate were possible between alternate and opposite leaves, and that there was such an adaptational urge that a plant began to progress in the direction of the latter. It is clear that once the leaves began to be nearly opposite, the urge would rapidly fall off, till at say 95 per cent of perfection it would be quite small, and almost infinitesimal at 99 per cent. How comes it then that opposite leaves are *exactly* opposite? How comes it that a drupe or a berry, a capsule or a schizocarp, is always the same in structure (incidentally, why has evolution made no apparent attempt at improving them?), and always complete? In the same way, a disadvantageous character would be unlikely to be completely got rid of.

It is, I think, safe to say that natural selection could not distinguish between 96 and 100 per cent of perfection, and that there must be some other principle that is responsible for the perfection that is always shown. By far the simplest explanation, and the only satisfying one at present, is that the perfection is due to a direct mutation. One can multiply examples to an almost unlimited extent.

For that matter, how is it that all the leaves upon a plant match one another so closely as they do, or all the flowers? The only explanation that the supporters of natural selection can give is that morphological considerations are more important in evolution than is natural selection (cf. pp. 120, 121). But how did natural selection begin to develop different types of leaf, and to make them so constant in size and form, and to put different types upon closely allied species (cf. the *Thalictrums* on p. 104)? There is not the faintest reason to suppose that evolution worked by different rules at different stages in its history, but the selectionists seem to think that if by aid of assumptions and supplementary hypotheses they can produce some kind of explanation of the phenomena seen at the present day, the past can take care of itself. What we are contending for is that morphological and anatomical considerations *are* more important than natural selection, and that the latter has not been, unless to some small extent or in some recondite way, responsible for the appearance of important structural characters. It acts upon what is given to it by the process of evolution, which goes on regardless of whether its products are acceptable or not. If they are killed out by natural selection, that is the end of that line, but others will appear. The simple and easy explanation of the phenomena of morphology is that they are due to mutations, which as a general rule probably produce a new form at one operation. To some extent at any rate, there is probably some definite factor in the parent, perhaps some arrangement or structure of the chromosomes, that determines what will appear in the offspring (and here again perhaps only in certain conditions, as for example possibly under the influence of cosmic rays). But we are as yet too completely ignorant of the whole subject to be able to hazard any definite opinion.

This test evidently gives very strong evidence in favour of the large mutations that are required by the theory of differentiation.

TEST CASE XI. THE EARLY STAGES OF CHARACTERS

One of the great difficulties that have always dogged the path of the supporter of natural selection as a cause of evolution, is to explain the beginnings of the various structural characters. This is a problem with which he has had little or no success. We have instanced many of the characters that divide species, genera, and

families, and have shown that even when fully fledged it is impossible to find any functional reason for their existence, and equally impossible to show why one should be preferred to the other, or to any (not commonly possible) intermediate, for any adaptational reason whatever: The adaptation to their surroundings that is possessed by all living beings is primarily an internal affair. Descending from ancestors not too far away in distance, they presumably in most cases possessed an adaptation that was not very different from that of their parents—at any rate those that did not possess it would soon be destroyed by natural selection. The adaptation might cover a greater or slightly different range of temperature or moisture, etc., that would enable them to reach places unattainable by the parents, thus ensuring ultimately a different distribution.

All evidence goes to show that adaptation is rarely shown in structural characters, and it will be of interest to draw up a short list of some of those things that were considered as adaptations in the writer's early days; hundreds more might be added:

Phyllodes in *Acacia*
Thorny roots in *Acanthorhiza*
Reversed leaves in *Alstroemeria*
Adventitious embryos
Self-burying fruit in *Arachis*
Hooked bracts in *Arctium*
Clasping hooks in *Artabotrys*
Cauliflory in *Artocarpus*
Pollinia in Asclepiadaceae
Thorns in *Astragalus*

and many more in genera beginning with A.

Red seeds in *Paeonia*
Gutta-percha in *Palaquium*
Horizontal fruit wing in *Paliurus*
Scaly fleshy fruit in Palms
Distribution by animals of stem joints in *Panicum*
Distribution of *Papaver* seeds by pores in capsule
Protogynous flowers in *Paris*
Neuter flowers in *Parkia*
Extrafloral nectaries in *Passiflora*
Biennial life in *Pastinaca*

and many more in genera beginning with P.

It only requires that one should quote such cases as these, which are not selected, but simply taken in alphabetical order from my *Dictionary*, to show how the idea of universal adaptation,

at one time held by almost everyone, has passed away, though natural selection, which is looked upon as depending upon structural adaptation, survives.

But the great difficulty which has always hindered the selectionist is to explain how natural selection got a grip upon the early stages of any of these characters. If they were produced in one operation, as differentiation demands, everything is simple, but in that case it is clear that natural selection can have little or nothing to do with their appearance. One must drop out natural selection as a guiding cause in evolution; it could get no grip upon the evolution of these structural features by gradual adaptation, and it could have nothing to do with it if they appeared fully-fledged. This test is in full favour of differentiation and what would seem the most probable order of things is that evolution, strictly so-called—the appearance of continually new structural forms—had little or nothing to do with adaptation of those forms to the conditions by which they were surrounded. They would inherit from the parents a reasonable probability of not being too unsuitable to survive at all, and it would then be “up to” natural selection gradually to fit them in minute detail for some particular combination of the conditions of life that existed near to the spot where they began, or to destroy them if this could not be done. Natural selection, in other words, strenuous though its action may be, has apparently nothing to do with the *evolution* of plants, though it has everything to do with the way in which they finally become best suited to some detail of combination of the conditions by which they are surrounded. Evolution and natural selection, in other words, may be represented as working more or less closely *at right angles* to one another, and the evolution goes on by large steps, as required by the theory of differentiation.

The theory of gradual formation of the structural features of plants seems to be left with little or no support, and a much simpler explanation of everything is provided by that of sudden appearance. People say that we have no evidence of such an occurrence, but we have no evidence of gradual acquirement, and a mere glance at the table of family characters in Appendix I will show that a great number of them are so divergent that they allow of no intermediate, and if one therefore *cannot* derive them by stages, they must have come in one step. And this is especially true when one finds that gradual adaptation will not do as a cause for change.

TEST CASE XII. ALTERNATE OR OPPOSITE LEAVES

Here is a familiar pair of contrasting characters, occurring in so many different places in the flowering plants that it is clear that they must be very easily acquired, while sometimes one of the two may be shown by a whole family, as are alternate leaves in the grasses. We have already shown (74) that many or most large families show, somewhere in their make up, exceptions to most of the characters that usually mark the family. Thus in Rubiaceae,¹ a very large family, one can find alternate, whorled, anisophyllous, pinnate, and gland-dotted leaves, leafy, and intrapetiolar stipules, dioecious, zygomorphic, and solitary axillary flowers, different male and female inflorescences, male and female flowers so different that at one time they were regarded as separate genera, flowers united in pairs, male flower 4–5-merous with female 8-merous, calyx convolute, imbricate, opening irregularly, with calyxulus, with one large sepal, 5-merous in male and 2-merous in female; corolla aestivation descending; stamens united, unequal, 8–12, two only with a 5-merous corolla; anthers opening by pores, or by valves, multilocular, heterostyled, with pollinia; ovary superior, united in pairs, 1- 3-5- 4- 6-10- or ∞ -locular; stigma 10-lobed; capsule both septi- and loculicidal or circumscissile, berry, schizocarp; endosperm none, ruminant; embryo with curved radicle, or with no cotyledons.

This is a very extensive list of exceptions, but most large families show something of the same kind, whilst even in the small ones divergence, usually just as pronounced as the divergences just given, is the common phenomenon, usually showing in them between the first two genera, or in the division into species if there be only one genus.

It is clear that if one were to combine in a group of plants a number of the “abnormal” characters that have just been given for the Rubiaceae, say alternate leaves with intrapetiolar stipules, dioecism, zygomorphic flowers in male and female inflorescences different from one another, the male 5-merous and the female 8-merous; calyx imbricate with one large sepal, corolla with descending aestivation, united, unequal stamens,

¹ Usual characters decussate entire leaves with interpetiolar stipules; regular flowers in cymes or heads, 5–4-merous; *K* usually open; *C* valvate or convolute; *A* 4–5, epipetalous; *G* (2), 2-loc., each with 1– ∞ ovules, style 1; fruit various; usually endosperm.

anthers opening by valves, ovary superior with ∞ loculi; fruit a schizocarp; embryo with no endosperm, no cotyledons, and curved radicle, a family would be produced that no one at any rate would imagine to have any relationship whatever to the Rubiaceae, and yet half-a-dozen to a dozen mutations might produce it.

Divergence such as that shown by alternate and opposite leaves, or any of the divergences shown in the list of "abnormal" characters of the Rubiaceae is a matter of extraordinary difficulty to explain by aid of the hypothesis of natural selection. Neither of the divergent characters has any functional value to the plant that anyone has ever been able to prove, or even to suggest; nor as a rule is there any possible intermediate, nor could it have any value or the reverse. Yet the divergences show in so many different places among the flowering plants that they must be very easily acquired; they are even found quite commonly between one genus and the next, or between some species and the next. But for such differences to be quickly acquired by natural selection, there would have to be some very pronounced advantage to be gained by their acquisition, and that is just what no one has ever been able to indicate. There is nothing to show that either opposite or alternate leaves have any advantage the one over the other, whilst an intermediate would still have alternate leaves, with a particular phyllotaxy. A point which is usually lost sight of, but is of great importance, is the difficulty of passing by aid of natural selection from say 95 to 100 per cent of perfection, already dealt with in Test case no. x.

This question of the relative value or disadvantage of a character is another thing that has been completely ignored during the long reign of natural selection. The great struggle for existence is among the seedlings, and a character that is of importance one way or the other to a seedling has a far greater relative value than for example a character of the flower or fruit which only appears in later life, when the plant is more established and has greater reserves of food and vitality. Leaves, for example, are much more important, individually and even collectively, when the plant is young. Even if a character were definitely disadvantageous it might still survive if it only appeared when the plant was old, whilst a disadvantageous character of any kind would probably be fatal to a seedling.

The only reasonable explanation of alternate and opposite leaves would seem to be to suppose that they are determined by

single mutations. The supporters of natural selection can only explain the exact nature of the oppositeness in the one case, or of the phyllotaxy in the other, by supposing that anatomical necessities are more potent than selection. Differentiation is much the most simple explanation, when one sees the well and exactly marked divergences that show so well, not only in leaves, but throughout the whole list of the characters that mark the differences in relationship of plants, and show that evolution has gone on.

TEST CASE XIII. STAMINAL CHARACTERS

One may work through the whole list of family, or even of generic characters, and find similar phenomena in all, inexplicable by the theory of natural selection or of gradual adaptation, though simply explained by differentiating mutation. Why in so many families and other groups should a great and important difference be that one has one whorl of stamens, while the other has two, or more? This dropping (or addition) of *whole whorls* of stamens cannot easily be explained upon adaptational grounds. Fewer stamens are usually regarded as a mark of progress in evolution. But why, for example, in a family mostly provided with ten, like the Caryophyllaceae, should the "advanced" members (which in actual fact look less advanced) only have five, with no indication, fossil or other, that they have ever had ten? Why does one find no trace of plants with nine, eight, seven, or six? If it be of any advantage to reduce the number of stamens, surely nine would be an improvement upon ten, and so on. Why should the whole whorl be got rid of with no trace of intermediate stages? The supporters of selection, when confronted with a morphological problem like this, are obliged to defend themselves by bringing in another supplementary hypothesis, this time a "tendency", supposed to exist in plants, to vary the number of the stamens by whole whorls at a time, which of course is more in keeping with the general morphology of the flower, though it is a very remarkable thing that this tendency is so widespread in flowering plants, there being extremely few cases, so far as the writer can remember at the moment, of intermediate stages in regular flowers. In other words, the supporters of selection admit that *morphological facts weigh more in evolution than does selection*, and they also admit that *large mutations can take place*. And whence did this tendency come, if it was not handed down from

the first ancestor of the whole family? Many of the families that now exist go back unchanged through the fossil records to more and more ancient times, or rather some of the larger and more widely distributed ones (the older, by age and area) do. There is no record of any preliminary stages in the development of a family, so that to imagine its characters as having been handed down from a first (single) ancestral form requires no stretch of the imagination, though it is not quite in keeping with the views derived from Darwinism. And as such large changes as the loss (or gain) of whole whorls of stamens are admitted, there seems no reason left why it should not be admitted that the family ancestor can appear by a single mutation.

One more example must suffice—the opening of the anther by slits, by valves, or by pores. Here again, one of these characters may be found in a whole family, in part of one, in a few genera, in one, or even in some species only in one genus. But where does natural selection get any leverage upon the character? In what way can it possibly matter to a mature plant which of the methods of anther dehiscence is employed, or to a young plant how its anthers are going to open at a later period? And how can the differences arise except by direct mutations? Gradual stages are almost inconceivable. The only adaptational value ever suggested is that the valve or pore might localise the pollen better upon a visiting insect, but unless the stigma is *also* arranged so as to touch the part bearing the pollen, there will be no gain, but rather loss. And this brings up the question of correlated characters, about which something must presently be said.

It is a matter of very great difficulty to account for morphological uniformity unless it arise by direct mutation, and unless it be handed down from above, as differentiation demands. How did the widely distributed tap root come into existence in so many flowering plants? How did the pore of an anther come to be like that of a fruit? How did leaves appear? Why have such a vast number of them much the same dorsiventral anatomy? Why are so many exactly opposite? Why are they in definite phyllotaxies? Why are some simple and some compound, why are they entire or toothed, palmate or pinnate, and so on? How could all the Cruciferae, and they only, get tetrodynamous stamens, which have incidentally no adaptational value, and have these together with the other well-marked characters of this family? Once more it must be admitted that morphology, or what the selectionists call tendencies, can override natural

selection, and that natural selection can do nothing to explain staminal morphology. The phenomena shown can only, at present, be explained by the supposition of sudden mutation, causing, for example, the loss (or gain) of five stamens, or the formation of a new method of dehiscence, etc.

TEST CASE XIV. THE BERRY FRUIT

The berry, as seen in the gooseberry or grape, is a well-marked and distinct type of fruit, the only hard part being the seeds, though there is a skin upon the outside. In the drupe, as seen in the cherry or the plum, the innermost layer of the fruit wall is hard, and the seed (kernel) inside this is usually soft.

There are berries in about a third of existing families, and as these contain more than half the total of genera, they are upon the large (old) side. But only a portion of their genera have berries. Berries occur all through the flowering plants, including, for example, the Araceae, Bromeliaceac, Rafflesiaceae, Annonaceae, Vitaceae, Myrtaceae, Ericaceae, Solanaceae, and Campanulaceae.

The fleshy fruits have always been a standby of the supporters of selection, who of course had to find adaptational reasons for phenomena, and supposed these fruits to be adaptations for dispersal of the seed. But if the seed be carried far, it will likely be dropped into another association of plants, where the competition will be equally severe, and the conditions probably different, so that it will be, if anything, at a disadvantage. One rarely finds another plant growing in an association to which it is foreign.

The berry and the capsule go together very much in related groups, but the capsule is much commoner, though it shows no adaptational advantage; the seed may be shaken out in a wind, but that is all. Some berried families, like Annonaceae, are common and widespread, but so are capsular families like the Caryophyllaceae. There is no evidence to prove any adaptational value in a berry. An instance which was sometimes brought up was the family Taccaceae, where *Tacca*, with a berry, is widespread through the tropics, and *Schizocapsa*, with a capsule, the only other genus, is confined to Siam and South China. But in Dioscoreaceae, one berried genus, *Tamus*, is confined to Europe and the Mediterranean, and has only two species; the other, *Petermannia*, with one species, occurs in New South Wales

(incidentally, therefore, the berry fruit must have been acquired independently of that of *Tamus*); while *Dioscorea*, with 600 species and a capsular fruit, is in all warm countries. Such cases are common in many different instances of various fruits. There is no evidence to prove that advantage is gained by the possession of a berry. In fact, as was pointed out in *Age and Area*, p. 21, nothing in the distribution of plants would lead any one to suppose that the "mechanisms for dispersal" have produced for the plants that possess them any wider dispersal than usual. *Tithonia*, with no pappus, and with mainly vegetative reproduction, spread as widely as, and not much more slowly than, the bird-carried *Lantana* in Ceylon, to which both were introductions.

The berry may occur in the whole or part of a family, in a few genera, in one, or in part of one. Considering the wide taxonomic separation of many of the berry families, it is clear that it is very improbable that all derived it from the same ancestor, unless the character could remain dormant for immense periods of time and change. It would rather seem to be one that is easily acquired, perhaps through some kind of kaleidoscopic change in the assortment of genes.

To explain why the berry is more common than the drupe, which is equally well adapted to transport by birds or animals, the selectionists have to bring up one of their many supplementary hypotheses, this time a "tendency" to vary rather in the direction of berry than of drupe, or again an admission that morphological facts weigh more in evolution than does selection. Presumably there is a still greater tendency to vary in the direction of the capsule, the least "efficient" fruit of the three. And whence did the tendency come, unless it were handed down from a common ancestor in each group, for whole families like Epacridaceae show a tendency towards the drupe, while their close relatives Ericaceae show a tendency chiefly towards the berry, but sometimes towards the drupe? Rhamnaceae have a dry fruit or a drupe, their close relatives the Vitaceae a berry. In the genus *Chironia* (Gentianaceae), mainly African, a small group of species in South Africa and Madagascar have a berry, the rest capsules. Why are there no berries in most of the generic area? This geographical localisation of structural features is common; e.g. in *Styrax*, the first genus to come to hand, most of the species have sixteen to twenty-four ovules, but there are some with three to five in Cuba and in Peru. It is a matter of great difficulty, if not impossibility, to explain such cases by

means of selection, but quite simple by mutational differentiation.

In the Caryophyllaceae, all otherwise dry-fruited (usually capsules), *Cucubalus* alone, with one species in Europe and Asia, has a berry. In Ranunculaceae, admittedly a very old and widely dispersed family, *Actaea* has a berry, while in Annonaceae all have berries but *Anaxagorea*.

In Myrtaceae, half the family, the Leptospermoideae, have a dry fruit, the other half, the Myrtoideae, a berry. How did natural selection, working upon the ancestors, ensure that all those with the berry should be more closely related to each other than to those with the dry fruit? Again "tendencies" have to be called in, but the differentiation answer is simple; an early mutation split off a genus with a berry from one with a dry fruit, and the descendants have inherited one or the other. An exception like *Cucubalus* is explained by a later mutation which involved a change of the chief fruit character of the family.

A great difficulty is to explain why the berry is always the same in its general structure, though it must have been picked out upon so many separate occasions. Why is it usually associated with the capsule, while the drupe is usually associated with the achene or the nut? In some families both may be found, but each keeps strictly to its own morphology, though under selection one would have expected more variety. How did capsules and other kinds of dry fruits that occur in close relatives all manage to change to berries of the same morphological construction? No intermediate forms occur, with few and slight exceptions. It is clear that the phenomena of berries are better explained by differentiation.

TEST CASE XV. ACHENES AND FOLLICLES

Here again are types of fruit found all through the classification of the flowering plants. Alismaceae have achenes, while their near relatives the Butomaceae have follicles. Half of the Ranunculaceae have one, half the other. Two of the three groups of Spiraeoideae have one, one the other. How were all these groups produced by natural selection with gradual adaptation? The question has hardly been properly thought out. How did the one fruit obtain, by this method, a completely closed wall, the other (when ripe) a completely open one? The value of selection would become less and less marked as the fruit approached perfection

in either of these respects. Yet both the follicle and the achene show perfection—the one in its complete closure, the other in opening from one extreme to the other of the wall, and only on one side. Why, again, did selection cause only one side of the follicle to open, and that exactly, while the pod opens with equal accuracy upon both sides? No adaptational difference between them can be shown to exist.

Ovules, again, cannot be developed in stages, from nothing to a complete ovule, though the reverse process is possible, but usually leaves some rudiments, which are not found in an achene. Nor can one imagine any transition—direct or through some intermediate form—from a multi-ovulate dehiscent fruit to a one-ovulate indehiscent. Nothing but mutation, and that considerable, could effect such a change, and as there is no adaptational reason behind it that one can conceive, a single mutation is more probable than a series of mutations. And again the morphological question comes up—why are all follicles structurally alike, and why were they produced in preference to pods or to achenes? In the author's opinion, nothing but a complete mutation of considerable size can have produced the difference, and nothing but inheritance from a common parent can have caused it to be shown by whole groups of species, genera, families, etc. In other words, differentiation is the most probable explanation, and natural selection in any direct form is out of the question.

Other types of fruit lend themselves to similar explanations, in which adaptation has but little if any part. It is, when one comes to think about it, a matter of extraordinary difficulty to show that the different fruits have any real adaptational value. What is the value to a tree like a Dipterocarp, which grows in dense practically windless forest, and often in a forest of one species only (pure stand), of its characteristic winged fruit? How could it, under the circumstances, have been developed by natural selection? Under gradual variation, all the sepals would vary alike, so that it must have begun with a mutation. And why should this be small, and not complete? In any case the calyx does not appear till the tree is perhaps thirty years old, and can anyone pretend that the struggle for existence between trees of this age and size is so severe that natural selection can get a leverage upon so slight a difference as the fact that two or three of the sepals are slightly longer? If anything, as the elongation will use more material, the longer sepals are more likely to be disadvantageous. If one say that the winged fruit gives the

advantage of dispersal to some little distance—an almost certain advantage if not pressed too far—how were the non-winged parents killed out, unless the winged offspring were also superior to them in some functional character that enabled them to kill out the parents upon ground which they already occupied, and where they had the great advantage given by the fact that they were already established there, and that transport of seeds in windless forest was a very difficult thing?

TEST CASE XVI. THE ORIGIN OF LARGE GENERA

Another troublesome problem for the selectionist is to explain how the method of selection gave rise to large genera. Upon what grounds of adaptation did *Senecio* come to have about 3000 species, and other genera also have enormous numbers, combining with the numbers a vast distribution over the earth's surface? If they owe their wide dispersal ("success") to adaptation, that adaptation can only have been generic. There are no characters in the individual species that one can point to as adaptive, and how could an adaptive and generic feature be produced in a genus formed from below upwards by the dying out of intermediates between it and its near relatives? If one of the species that were going to form *Senecio* had a really fine adaptation, one would expect it to go ahead and rather form a genus of its own than simply join the rest. The bulk of the species in these big genera are local in distribution, and it is far simpler to explain the whole matter by differentiation and by age, which simply says that on the average the wider-dispersed species are the older.

Other remarks on "generic" adaptation will be found on pp. 18, 59.

TEST CASE XVII. SOME MORPHOLOGICAL PUZZLES

Even in the comparatively few cases where a plant shows some structural feature that may be looked upon as a definite physiological advantage, like the tentacles of the Droseraceae, natural selection is hard put to it to explain how they could be formed by gradual adaptation. How, for example, did it produce the marvellously sensitive tentacles of *Drosera* itself, when the first steps

in their formation would be absolutely useless, and when their movement would be of no value until it was perfected? Why did it also evolve *Drosophyllum*, with no movement, and with two kinds of tentacles? And how did it place the tentacles in straight rows, and make them all alike? Again the reply has to be that morphological considerations inherent in the plant override the effects of natural selection. And why so, when they must themselves have been derived in the same way? Further, how did natural selection evolve, in the same small family, *Aldrovanda* and *Dionaea*, with leaves that close up like a book? One does not expect to find, in so small a family, such marked differences; it reminds one of the Podostemaceae. The differences are much more marked than in a whole large family like the Compositae or the grasses.

There is almost no end to the inexplicable difficulties in structure that can be brought up for the selectionist to try to explain. Here, for example, are a few picked out in hastily running through the list of family distinctions given at the end of my *Dictionary*:

- The windows in the leaves of Aponogetonaceae.
- The complex inflorescence of *Zostera*.
- The three-ranked leaves in Cyperaceae.
- The spiral or disc-like flowers of *Cyclanthus*.
- The pitcher of leaves in many Bromeliaceae.
- The resupinated flowers of Orchidaceae.
- The Equisetum-like stems of Casuarina.
- Chalazogamy.
- The explosive stamens of Urticaceae, etc.
- The integumentless ovule of Opiliaceae.
- The tetrodynamicous stamens of Cruciferae.
- The pod of Leguminosae (why not a follicle?).
- The obdiplostemonous stamens of Oxalidaceae.
- The cyathium of Euphorbia.
- The explosive capsule of Impatiens.
- The stinging hairs of Loasaceae.
- The asymmetrical leaf of Begonia, etc.
- The one-sided flowers of Lecythidaceae.
- The vivipary of Rhizophora.
- The free-central placenta of Primulaceae.
- The corona of Asclepiadaceae.
- The scorpioid cyme of Boraginaceae.
- The didynamous stamens of Labiateae, etc. (why do they match in several different families?).
- The four nutlet fruit of Labiateae.
- The pappus of Compositae.

Nothing but common descent will explain most of these, and, if so, the *family* must have been very ancient, and why are there no fossil traces of any family formation, which must have gone on for an immense period of time if they were made by the method of dropping intermediates involved in the explanation by natural selection? Not only so, but the bulk of the characters described in the list above, to which hundreds more might be added, are such that they must have arisen at one step; either no intermediates are possible or they would have been completely useless, and therefore incapable of being chosen by selection.

TEST CASE XVIII. THE SMALL GENERA

If the small genera are to be regarded as failures and relics, it is somewhat remarkable the way in which they are closely grouped round the large ones, usually regarded as the successes. If one take the two largest genera in a family—the two which upon the theory of differentiation represent, *upon the average*, the result of the first throwing of a new genus by the original genus which was the first parent of the family—one commonly finds them marked by a large divergence. But this same divergence is shown (cf. p. 84) by the groups of "satellite" genera round them, and these include the bulk of those which are classed as relics. Their characters are the chief characters of *Ranunculus*, for example. Upon the theory that *Ranunculus* owes its success to some of its visible characters, we should expect these to be the characters. Why then are the satellite genera so "unsuccessful"? Very few small genera are known which are not classed in the sub-families which are usually marked each by a fairly important genus at the head. And why should this be, unless the satellites were derived from the large genera? If this happened in the earlier days of the big genera, it is somewhat remarkable that one so rarely finds any fossil traces of the little ones, and if in the later days, why should the big genera throw off, at such a late period, genera that were only to be relics or failures? It seems much more probable that the small genera were thrown off at a late period in the life of the large ones, by some larger change than would give rise merely to new species, but a change that could not have been the result of the work of natural selection. The test favours differentiation much more than it favours natural selection.

TEST CASE XIX. CORRELATED CHARACTERS

The difficulty of imagining that evolution worked in the direction from species towards genus is vastly increased when we come to deal with the correlations that exist in the characters of the various flowering plants. Though there is usually no conceivable adaptational reason behind them, the characters of whole families, for example, usually go together in groups, for whose connection we can see no reason at all, unless it be simply that the common ancestor happened to possess this combination. In the grasses there go together alternate leaves, in two ranks, a split sheath, a ligule, jointed stems, a spikelet inflorescence with glumes and paleae, and so on. How did natural selection pick out all these characters to go together, even if by any stretch of the imagination one could imagine it picking out a split sheath in a grass, and a closed one in the allied sedges, or in fact any of the other characters? They must have been derived from a common ancestor, and if so, where did selection and adaptation come in? If all the structural characters of a family, those characters in fact that mark it out as a family, are hereditary characters, there is comparatively little room left for any adaptive characters at all and once again it is clear that morphological characters override selection. Even if there be no specially adaptive characters in the grasses or the sedges, there must have been some disadvantageous ones in the plants that were suppressed in the struggle for existence which made the wide gap that now separates these two allied families. But is it conceivable that a series of intermediate forms with, for example, a sheath partially split should have been so inferior that they were killed out? Still more difficult is it to imagine intermediates which showed intermediate characters in *all* the characters of difference, if one suppose for an instant that such a thing were possible; there can be no intermediates between 2-ranked and 3-ranked leaves, or between the two types of inflorescence, etc. Direct mutation must have occurred in many cases; and gradual adaptation is hardly conceivable, especially when so many characters have to go together, and each has to be brought to the point of perfection (cf. p. 114).

The larger the family, the greater on the average is the variety of conditions that it occupies, as may be seen in the grasses. Yet natural selection is supposed to form a family by gradual adaptation, and it is therefore clear that, as indeed the geological record shows, families must have come *very* early in evolution, and the

great variety of conditions in which the large families now live must have been due to subsequent adaptation. But this leads to the somewhat surprising conclusion that adaptation must have been very strongly in evidence in early days, with a corresponding amount of destruction to separate the families, for which we have no evidence.

Or why were one-fifth of the flowering plants picked out to have only one seed-leaf instead of two, to have the parts of the flower in threes instead of in fives, to have leaves with parallel veins instead of netted, and to have so different an internal anatomy, with no simple process of growth in thickness? And still more difficult is it to explain, on the theory of gradual selection, why all these characters should go together, when they have no adaptational meaning, either singly or in combination. One can conceive that the anatomy of the Monocotyledons was definitely disadvantageous, which may explain why there are comparatively few trees among them; yet the palms seem successful enough, or the bamboos. But the important fact remains unexplained, and not to be explained upon the theory of gradual selection, that, as already pointed out, the Monocotyledons maintain their proportion of one in five in all important parts of the world.

An interesting case of correlation incidentally showing the totally useless nature of many, or nearly all, of the generic and specific characters may be seen in the genus *Pyrenacantha* in Icacinaceae, which has a drupe with the *inner* side of the shell thorny; correlated with this are definite holes right through the endosperm to leave room for the spines. Here is a case that it would puzzle the selectionist to explain, and there are many more. And it is somewhat difficult to imagine intermediate stages.

To try to explain these correlations in terms of gradual adaptation is a practical impossibility, and if they were formed at one step, how does adaptation come in? Take, for example, the case of climbing plants, already considered (p. 57). Or take parasites, which must also have been a later development than non-parasitic plants. Until the sucker has actually penetrated the host, the habit will be of no value, so how did it begin under the operations of natural selection with gradual adaptation? And incidentally, such parasites as the fungi live almost entirely within the host, where the conditions must be more or less the same for all, so how did they come to develop such numbers of species with definite structural differences? How did the ordinary

leaf come to develop stomata, intercellular spaces, palisade and spongy tissue, and the fine network of veins, and how did it develop these last in so many patterns of netting, parallelism, etc.?

Correlation, if large, implies that most characters have no bearing upon natural selection, and do not interfere with the results gained by the first character. And as differences in one character only do not usually cause mutual sterility, one wonders how that comes to be so common a mark of specific difference.

One must look with great suspicion upon such easy interpretations of things as calling them direct adaptations. If they were formed as such, the work was too complicated for natural selection. It is more probable that they were formed at one step, and not being harmful, were allowed by natural selection to survive.

CHAPTER XII

SOME TEST CASES BETWEEN THE RIVAL THEORIES

C. TAXONOMIC

THESE cases might equally well go under morphology, for taxonomy or systematic relationship is founded upon that subject. The separation is simply used to prevent the morphological chapter from growing too large.

It is of interest to note how easily the axioms of taxonomy that are given by Darwin in the *Origin of Species* are explained by the theory of differentiation. The first one, for example,

Wide-ranging, much diffused and common species vary most
fits in admirably with much that has been said above, and with what the writer hopes to bring out in another book. It should also be compared with Guppy's remarks about the wide-ranging species that so often accompany endemics, and with what is to be said about the wide-ranging species that so often do the same thing in India (p. 158). One may also refer to what will be said about contour maps (p. 149).

The current view is that the large and widely distributed genera and species are the "successful" ones, and that they are breaking up into new species by the formation of what as yet are only small varieties. On the view taken by the adherents of Darwinism, the Linnean species of the taxonomist is an abstraction, consisting of an agglomeration of smaller forms that really breed true, and that may be more or less well assembled into a Linnean species which can be reasonably well marked off from others that are closely related to it. But upon the theory of differentiation the case is turned the other way round. There is little or no doubt that many of the very local endemic species, which are often supposed to be relics, but which upon the theory of age and area are regarded as young beginners, are well and clearly marked Linnean species. Take, for example, the *Coleus elongatus* (p. 24), or the Indian local species described on p. 159. The whole species, in cases like the *Coleus*, is made up of so few individuals that it is impossible that there should be a great range of variation, for mere lack of numbers. It is *after* the formation of the

species, when it begins to move into a greater range of conditions and climates, that it begins to show a range of smaller forms, which to the writer represent later stages in the continually diminishing mutation that began with the formation of the family, the genus, and this particular species. It is to be noted also that the great range of form only shows as a rule in species of the larger (or older) genera. When it does occur in species of small genera, the genus usually has a wide range, showing that it is probably old in its own circle of affinity.

It is very difficult to see why on the Darwinian scheme the only genera of a very small family ("relics") should be separated by as large distinctions as those that separate the sub-genera of a large family (p. 112), and why those distinctions should be so often such as are incapable of having intermediates, like many of those given in Appendix I. And it is equally difficult to see why the species of a single genus making up a family by itself should be grouped by such wide divisions as are instanced upon p. 79, again distinctions that do not often admit of intermediates.

From the differentiation standpoint, the puzzle presented by these little "Jordanian" species, such as were described in *Draba*, for example (22), and which no stretch of imagination can show to be the commencement of new species derived by gradual adaptation upon the Darwinian plan, becomes quite simple. They are simply the last wavelets of the great disturbance that was made when the parent of the Cruciferae was formed from something else by a "large" mutation that gave it tetradynamous stamens and the rest of the outfit of the Cruciferae.

The second axiom is

2. *Species of the larger genera in each country vary more frequently than the species of smaller genera.*

Here again the variation was put down to the "success" of the larger genera, which were going on to develop new species, but, as explained above, it is much simpler to put it down simply to the age of the genera and size or area of the species, the larger being older, and having had more time to develop smaller mutations than that which gave the ordinary species.

3. *Many of the species included within the larger genera resemble varieties in being very closely but unequally related to each other, and in having restricted ranges.*

This is exactly what shows in the hollow curves. In the large genera there is a great proportion of species of small area, far

more than of medium or large (cf. p. 98). In places where there are many of them close together, as with the big genera *Eugenia* or *Memecylon* in Ceylon, they are all more or less closely related, though many of them are quite good Linnean species. Attention may also be drawn to the "Jordanian" species in big genera like *Draba* or *Hieracium*.

4. *The varying species are relatively most numerous in those classes, orders, and genera which are the simplest in structure.*

5. *As with species, so with genera and families... upon the whole those are the best limited which consist of plants of complex floral structure.*

6. *Those classes and families which are the least complex in organisation are the most widely distributed, that is to say that they contain a larger proportion of widely dispersed species.*

7. *This tendency of the least complex species to be most widely diffused is most marked in Acotyledons (Cryptogams) and least so in Dicotyledons.*

8. *The most widely distributed and commonest species are the least modified.*

All these latter axioms go together, and obviously fit exactly with what would be expected under the law of age and area, which makes the older (and therefore on the whole the simpler) forms to occupy more area than the younger and more complex. The fact that all these dicta are axiomatic does not say much for the supposed continual improvement in adaptation under the operations of natural selection, especially as this theory also tries to explain greater range by the same improved adaptation. The whole of the axioms are rather against the Darwinian theory of progress, and are in much better accord with that of differentiation.

TEST CASE XX. THE POSITION OF THE LARGEST GENERA IN A FAMILY

On the theory of natural selection, one can make no prediction whatever as to the position in the classification of a family of the largest genera in it. There seems no reason whatever in anything that we know about them which should show that they should be near together, or that they should be far apart. But upon the theories of differentiation and age and area, the largest genera should on the whole be the most widely separated, in-

asmuch as they will have inherited their characters from the point that is the farthest back that is possible—the earliest mutational divisions that took place in the family concerned.

In deciding this point we must, of course, work with the keys with which the taxonomists have provided us, but the latter have, of course, taken the greatest possible pains to find the most widely different characters that mark the different groups. In their keys they usually begin with very divergent characters, inasmuch as they have learnt by experience that these mark the largest divisions in the great majority of cases, separating the genera first of all into two large groups. These groups again are separated by the most different characters that can be found, but which do not mark the whole, but only a part of the first group. And so on, breaking up the family into allied groups within allied groups—the general principle of all classification.

One will, therefore, expect that the first one, two, or at most perhaps three separations that are given in any ordinary good key will separate not only the chief sub-families or tribes, but also the largest genera, and one will expect these to be separated by such distinct and divergent characters that there will be little or no difficulty in picking them out from one another. When such difficulty occurs, it should be in genera that have become so large that their outlying species, which will have been liable to more change than the earlier and more "genus-like" ones, have in one or two cases reached almost to the overlapping point. We should expect, but have not had sufficient time to test the matter, that these difficult species would prove in general to be comparatively local, that is to say, on the whole, the youngest species in their genera, which will have gone through the greatest number of mutations since the first throwing of the genus.

As a test of this case, we may take the family Ranunculaceae, which is already described from this point of view in the chapter upon Differentiation. The first division of the family in most keys throws the largest genera on both sides. Here, for example, *Aconitum*, *Aquilegia* and *Delphinium* have follicles, and *Anemone*, *Clematis*, *Ranunculus* and *Thalictrum* have achenes. But as the two actually largest genera are *Clematis* and *Ranunculus*, separated by the very divergent character of opposite or alternate leaves, it is possible that this was the very first mutation, and that *Clematis* mutated off no other genera with opposite leaves. Or yet again, we must always bear in mind the possibilities of such complex mutations as are indicated in Hayata's

work (16). All that we are at present contending for is that species and genera were formed each at one mutation, and that the change went downwards to the species, not upwards from it, as required by natural selection (of course a genus cannot exist without one species).

In the same chapter (ix) we have also described the sub-family Silenoideae of Caryophyllaceae, and shown that the first split in the key throws *Silene* with 400 species to one side, *Dianthus* with 300 to the other.

This phenomenon, which is so common that it must have a reason behind it, occurs in a great number of cases. Picking up a few copies of the *Pflanzenreich* as they come, the first is Marantaceae, where *Calathea* and *Maranta*, the two largest genera, are separated by the first split. In Myrsinaceae, *Ardisia* goes one side and *Rapanea* the other. In Amaranthaceae, *Alternanthera* goes one side, *Ptilotus* the other. In Cyperaceae *Cyperus* and *Carex* do the same; in Eriocaulaceae *Eriocaulon* and *Paepalanthus*. In Hydrophyllaceae, *Phacelia* and *Nama* go one side, and *Hydrolea*, with only nineteen species but very wide distribution, the other. In Monimiaceae (p. 33) *Siparuna* goes one side and *Mollinedia* the other. And so on indefinitely.

It is thus clear that as the position of the largest genera, and their sharp distinction in the great majority of cases, agrees with what is required by the differentiation theory, while that of natural selection can give no idea where they will be found in a family, the evidence of this test is in favour of the former. Inasmuch as the classification of animals is equally possible, with equally good results, when conducted upon the same lines as that of plants, and as it shows the same hollow curves, it would seem highly probable that the same general principles have guided the evolution that has gone on in them also.

TEST CASE XXI. THE POSITION OF THE LARGE FAMILIES

We may even carry the supposition outlined in the last test a stage farther, and apply it to families, saying that the very large ones will be very widely separated. We are still so undecided about the proper classification of the larger groups of plants that it will not do to push this very far, but one may note that the three largest families of all, from the latest figures in my possession, are Compositae (18,089 species), Leguminosae (12,754) and

Orchidaceae (10,088). Here, incidentally, is a case for the provisos with which I hedged age and area, that one must never compare anything but close relatives as regards age. To say that the Compositae are older than the Leguminosae is obviously a statement with nothing to back it. But the fact is there, that one could not easily find greater divergence than is shown by these three families, which incidentally contain nine out of twenty-nine of the genera containing over 500 species each. If we go over the first ten families in point of size, we find the fourth, Rubiaceae, to have one of these genera, the fifth, Gramineae, one, the sixth, Euphorbiaceae, three, the seventh, Melastomaceae, two, the eighth, Labiate, one genus, while there are none in the other two. But these eight families contain seventeen out of the twenty-nine of these big genera, and most of the rest are in large families, though there are a few small ones which contain very large genera, like Begoniaceae.

The twenty-seven large families with over 1500 species are Acanthaceae, Apocynaceae, Araceae, Asclepiadaceae, Boraginaceae, Bromeliaceae, Caryophyllaceae, Compositae, Cruciferae, Cyperaceae, Ericaceae, Euphorbiaceae, Gesneraceae, Gramineae, Labiate, Leguminosae, Liliaceae, Melastomaceae, Myrtaceae, Orchidaceae, Palmaceae, Rosaceae, Rubiaceae, Rutaceae, Scrophulariaceae, Solanaceae, Umbelliferae. It will be seen at once how wide a range they cover in the classification, in fact touching all important parts of it.

The evidence of both these test cases is strongly in favour of divergent mutation, forming the whole family or genus at one step.

TEST CASE XXII. DIVERGENCE OF VARIATION. SYSTEMATIC KEYS

In making keys to families or genera, by whose aid one may determine the relationships and position of the plants with which one is dealing, the taxonomist is concerned with providing the easiest and most certain method of so doing. And it is a very remarkable fact, that has hardly been sufficiently recognised, that it is usually possible, without any very great difficulty, to make a *dichotomous* key (sometimes trichotomous at certain points), beginning at the top with characters that will separate one sub-family from another, and working right down through tribe, genus, and species, to variety, in the same way. This fact, which upon the theory of differentiation *must* occur, does not

agree very well with the theory of natural selection, nor with that of gradual adaptation. There is no doubt that as one proceeds up the scale from variety, the divergence of the characters becomes greater and greater, and upon these latter theories it is a matter of extraordinary difficulty to explain why the destruction of the intermediate forms should proceed in such a way as to leave groups that present divergences that are more and more marked the higher that one goes in the scale, while at the same time they are quite simple divergences, such as ovary uni- or multi-locular, anther opening by slits or by pores, leaves opposite or alternate, and the rest. Nothing but differentiation can at present explain such phenomena.

TEST CASE XXIII. DIVERGENCE FROM USUAL FAMILY CHARACTERS

It is a very noteworthy thing, which the selectionists have found so difficult of explanation, that they have had to fly to their usual refuges, that plants that show great divergences from the characters usual in their families occur, not in the small families (relics or failures) but almost only in the large ("successful") ones. We have given an instance from the Rubiaceae on p. 118 and the matter is discussed in detail in (74, p. 621). In the large families one would be inclined to expect constancy, for if it were settled by the early ancestors of Papaveraceae, for example, that a hypogynous flower was the best, why did *Eschscholtzia* adopt a perigynous one? *Solanum*, by far the largest genus in its family, opens its anthers by pores, while most of the rest open by slits. Is this the generic adaptation that caused *Solanum* to become so "successful"? One could go on bringing up cases like these, and there is no escape from the conclusion, so far as our present knowledge goes, that characters of all kinds, however important in classification, may be acquired by single genera at any stage, so that their acquisition is evidently easy, and must almost certainly be due to direct mutation. Like all the other tests this speaks in favour of differentiation.

TEST CASE XXIV. PARALLEL VARIATION

A puzzling case, which the natural selection theory can in no way explain, except by the favourite suggestion of "tendencies", is the parallel variation that so often may be seen. A good instance is afforded by the related families of Eriocaulaceae, Centro-

lepidaceae, and Restionaceae. Each family makes its first division (in some classifications) into Haplanthereae and Diplanthereae, or groups with monothealous and with dithealous anthers, a well divergent and clearly marked division. In the Eriocaulaceae the Diplanthereae contain half the genera of the family, including *Eriocaulon* and *Paepalanthus*, which are by far the largest genera, while the Haplanthereae include only very small genera, whose species make only about 2½ per cent of those in the other group. And whilst the Diplanthereae cover the warmer parts of the world, the Haplanthereae are found only in warm America. In the Centrolepidaceae and Restionaceae, on the other hand, the larger group is the Haplanthereae. In the former, they include five genera and thirty-five species, against one and two in the Diplanthereae; and in each case the distribution is much more extensive.

There is no conceivable reason why dithealous anthers should suit America better, and monothealous the Old World, and yet the former are more common in the one, the latter in the other. It is clear that we must be dealing here with a divergent mutation, and that one family began with dithealous anthers, the other two with monothealous, and that probably each one subsequently split off the other division. The Eriocaulaceae, for example, beginning dithealous, spread over the world, but split off the monothealous group in America. Perhaps the splitting off was too late for the plants to cross to the Old World in any case, or it may have been that as we have elsewhere explained the early growth and dispersal of the new forms was too slow for them to be in time to cross.

Cases of the same kind, showing exact parallelism, are very numerous indeed. To take a few examples, the Marantaceae divide into a group with 3-locular ovary, and a group with 1-locular, and each of these divides into a group with two lateral staminodes, and a group with one. In Amaryllidaceae both the groups Amaryllideae and Narcisseae divide into groups with many ovules and with few, whilst this is the first division in the related Haemodoraceae. In Araceae, most of the principal groups divide into groups with endosperm and without. In the Palmaeae, several widely separated groups have fan leaves, others feathers. And so on, in hundreds of cases.

This phenomenon has always been a great difficulty to explain upon the theory of selection, for it makes it obvious that none of these characters—for example, those of climbing plants, else-

where described (p. 57)—can be difficult of acquisition. In many cases differences of this kind can be seen between closely related species. The only reasonable explanation is that their appearance has nothing directly to do with adaptation, and is the result of simple mutation, which is so very commonly divergent. In other words, this phenomenon, which is so very common throughout the vegetable kingdom, and which is not unknown in the animal, is an expression of the operations of differentiation, not of those of natural selection, while at the same time it suggests complications in evolution, perhaps like those suggested by Hayata (16).

TEST CASE XXV. GREATER LOCALISATION OF HIGHER TYPES

That the higher groups of organisms, for example the flowering plants, are more localised in distribution than the lower groups, such as the ferns, has long been an accepted axiom, and has often been put down, as for example by Darwin and by the author, largely to the greater antiquity of the lower groups. But if we carry this principle into greater detail, it is clear that if in any family or group of families some forms are more widely distributed than others, those forms should on the whole be the older—the principle for which the author contended in the hypothesis of age and area. But the explanation of geographical distribution that is given by natural selection, or gradual structural adaptation, involves the assumption that the forms that have spread the most widely will be those that are the best adapted, though to what they are adapted is left vague. Upon this view of evolution, one cannot regard genera like *Carex*, *Draba*, *Eryngium*, *Eugenia*, *Euphorbia* or *Senecio* as being poorly adapted when compared with the vastly more numerous smaller and more localised genera. But when one asks why such families as Cephalotaceae, Hydnoraceae, Nepenthaceae, Orobanchaceae, or Sarraceniaceae have not spread widely, with such “adaptations” as they show, one is told that their adaptation is too special to have allowed them to do so. But why should *Nepenthes*, for example, be well suited to the variety of conditions with which it meets in Malaya, Ceylon and Madagascar, and yet not capable of withstanding those of tropical Africa, America, Polynesia or Australia? The Sarraceniaceae, with not dissimilar adaptations, can do so, and do not occur in the Old World. It is not even as if there were only one species in each of the genera; there are scores

of *Nepenthes*, for example, so that the adaptation which enabled the genus to spread must have been generic, perhaps principally the pitcher. But if so, why could not some species have been able to live in America, or some *Sarracenia*s in Europe? No feature can be pointed out in the pitcher or any other character of *Nepenthes*, which should limit it to its present distribution. *Sarracenia*, as pointed out on p. 56, is naturalised in a bog near Montreux. Nothing but an explanation based upon age and area will answer the innumerable questions like this which come up in a study of distribution.

This feature, that the enormous distribution of large genera like *Carex* or *Senecio* can only be explained by generic adaptation, if one is to accept the "explanation" given by natural selection, is a very fatal objection to the theory. The six genera above mentioned average a thousand species each, and it is a very astonishing thing that the original adaptations should have been such that they remain in their progeny after all this degree of change.

As in general we are not always very sure of what we mean when we say that one genus is more complex than another, and as opposite views are frequently expressed in any particular case, it is fortunate that in the Podostemaceae and Tristichaceae we have families where it is almost impossible to be in doubt, for the obvious change that has gone on is from a slight to a great dorsiventrality. The comparatively primitive forms are widely dispersed, the more modified are local.

It is fortunate that we have this evidence, for usually it is not easy to draw conclusions from the morphology. It is often said, for example, that reduction in number of stamens and carpels is evidence of progress, yet we can find the widely dispersed species in some families showing the one thing, the narrowly dispersed in others. For example, with leaves alternate/opposite, the Erythroxylaceae go one way, the Caryocaraceae the other; with flowers regular/irregular, Aristolochiaceae and Commelinaceae go one way, Dichapetalaceae the other. With corolla valvate/convolute, Quiinaceae go one way, Cistaceae the other, with stamens ∞ /few we have Loasaceae and Papaveraceae/Quiinaceae and Velloziaceae. With carpels ∞ /few, Papaveraceae/Portulacaceae, and so on indefinitely.

CHAPTER XIII

SOME TEST CASES BETWEEN THE RIVAL THEORIES

D. GEOGRAPHICAL DISTRIBUTION

THIS group of test cases is placed last, as the author is at present writing a book upon geographical distribution, and many tests that could be given would require such long quotations from that work that they are not suitable to the present one.

Geographical distribution, properly so called, unlike ecology, is so bound up with the question of the origin of the species with which it deals, that it must be based upon some theory of that origin, and this theory must be able to explain all or most of the well-known facts of distribution without serious difficulty. To take one case only, special creation could not explain the relationship of species in one country, say Britain, to those in another far removed, like New Zealand. It was succeeded by natural selection, which, however, did its great work rather in establishing evolution, and thus opening out a great field for research, than in explaining geographical distribution. Not only did it show that resemblances were mainly due to relationship, but it also seemed to show that wide dispersal, or successful spread, as it now began to be called, must be due to unusually good "adaptation". This latter, however, has never been proved. The struggle for existence was undoubtedly in full operation among individuals, but even there, chance had probably a much greater effect, for the great struggle was amongst the young, and better water supply, better light, better soil, earlier arrival or germination, etc., etc., would have greater effect than any slight advantage that the young plant could carry in itself.

Natural selection *had* to explain geographical distribution, and there seemed no other way to explain it than by transferring the hypothesis from individual to species; but as yet we have no evidence in favour of this great assumption. We do not know that species or varieties can come into direct competition with one another as units in a war à l'outrance, especially as in general they will occupy more or less different areas, and one would hardly expect that species B would follow its defeated rival A into all its habitats, and kill it out there. If this was the way in

which one species won at the expense of another in the struggle for existence, one ought to find many cases of this internecine struggle going on in many places, but one does not. One only finds a struggle between individuals, in one place a member of species A being successful, in another a member of B.

The supporters of selection say that the intermediates, which also came into the competition, have been killed out, and that the two survivors are now adapted to slightly different conditions. This is of course possible, but it is a very remarkable thing, when one thinks of all these processes going on gradually, as must be the case under the old theory, that one does not find intermediates in the fossil deposits. What are sometimes called intermediates are really a very different thing, usually plants with some of the characters of one, some of another, really a very good argument for differentiation. And further, why does one not find intermediates at the present date? Is the competition now finished? One would expect to find some cases in which it was still going on. We have already seen that in a great number of cases, especially in those high in the scheme of classification, intermediates between the characters are actually impossible, and how mutation, crossing the whole gap between the two at one operation, is the only probable explanation. It is no argument in favour of this supposition, that species can act as units, to say that masses of men of (to some extent) the same race, like the Fijians or the Hawaiians, can act together as units. Man has sufficient intelligence to be able to combine to some slight extent, though it is a somewhat ironical commentary upon that intelligence that his chief and most efficient combination is for the purpose of making war, whose results are more against natural selection than for it.

The new and better adapted form was supposed to kill out the less well-adapted parent. But as they would usually meet only at the edges of their respective territories (p. 13), where they would tend to cross, and to lose their identity, it would require a vast amount of time for the new one to invade the territory of the unimproved parent, and to kill it out entirely. Almost certainly examples of the old species would be left in many different spots, where they had been overlooked, a feature which in actual fact is very rarely seen.

Incidentally, the new species would have to kill out all the hybrids at the meeting place of the new and the old, and if it had not crossed the "sterility line" it would continue to make

more hybrids, so that the only result of an incipient species trying to gain territory at the expense of its parent would be the continual formation of hybrids. Only when the sterility line had been crossed would the new species really be able to conquer the old, and to supplant it. But it is very hard indeed to see how this line can be crossed in any case without a large mutation that will create a new species at one step; one cannot easily imagine a species gradually crossing the line of sterility, nor even a series of small mutations doing it.

There is evidence to show that on the whole the parent will continue to gain in dispersal upon the offspring (66, p. 34), and if this be so, it could not be altogether killed out, unless the assumption that the offspring, by becoming better adapted to place A, became thereby better adapted to B, the home of the parent, were correct. There is little or no evidence that a species, and still less a variety, fights as a whole, and an organisation that is based upon such a contention, as so much political organisation is at present based (the operation of the dead hand, so well described in Woolf's *After the Deluge*, chap. 1), has no strong scientific backing.

To carry out evolution by natural selection involves a vast amount of destruction, for which we have no evidence in fossil botany or elsewhere, whilst such destruction is not involved in the theory of differentiation. To try to explain the phenomena of geographical distribution upon the supposition that one species has conquered and destroyed another is to build upon a somewhat insecure foundation. It has hitherto been assumed that a widely dispersed species owes its dispersal to the fact of its superior adaptation. But to *what* is it adapted, and how in country A did it become adapted to the conditions of country B? If its range be large, it must come into greater variety of conditions than if its range be small, and that must mean that as it moved about it became functionally adapted to all these conditions in turn, but that is no proof that in becoming adapted to B it retained the adaptation to A. But in any case much time must be allowed, i.e. that wide-ranging species are usually old, a supposition that agrees with age and area. The more local species, which do not occur in such variety of conditions, are the younger. It would, therefore, form a much more probable explanation to say that the widely dispersed species were the old ones, dispersed before the land was broken up into its present divisions, and before the climates showed so much differentiation as they do at the present

time. These old forms, being simpler, would show less adaptation to any particular conditions, but would probably show greater *adaptability*. This conception agrees much better with the facts, which go to show, as was pointed out by Darwin, that the organisation of the widely dispersed species is definitely simple rather than complex, when allies only are considered, as must always be the case in general comparisons with regard to age (cf. p. 29) or dispersal.

All the facts that are known go to show that in the majority of cases an individual plant arises in a place at no great distance from that where its parent is to be found. If it survive, and grow to the reproductive stage, one may conclude not only that chance has favoured it, but also that it has probably passed through the sieve of natural selection, and may be said to be more or less suited to that locality. If the seed, however, be carried to a greater distance than usual, say to more than 250 or 500 metres, whether it prove so suited to its new locality as to survive and reproduce there will depend upon a number of things. It may find a good deal of difference in the soil, though not perhaps in the climate, and if it has been carried beyond the range of the particular association of plants in which it has been growing, there may be considerable biological differences, which again may be accompanied by soil changes and the like. It will then be a matter of chance whether it prove suited to the new locality—to talk of adaptation in a seed only newly arrived, though it may prove *suited* to the place, would be going too far. If it survive to the reproductive stage, it will probably have begun by that time to adapt itself to its new surroundings. In each successive generation this adaptation will continue, until, after a time which is probably different in each case, it has again become fully adapted to local conditions. This process may continue until, after a very long period, the species may cover, as does *Hydrocotyle asiatica* (p. 58), a very large area of the surface of the globe. If we abandon the notion that adaptation is shown by the structural characters of plants, but that it is much more the physiological or functional adaptation that must go on in any plant that moves about and comes continually into new conditions, the supposition that we have just given explains, with the aid of age and area, why species are arranged over the world in "wheels within wheels", why the largest numbers are found upon the smallest areas, and those that occupy larger areas decrease in a "hollow curve".

If the conditions begin to change in any place, the new ones may encourage some plants, and discourage others, so that natural selection may in time effect a change of the local flora, some plants coming in from other near-by regions where conditions are more or less like those which now obtain in the locality under consideration, and some of the local ones perhaps dying out in that region. Possibly, even, under the stimulus of changed conditions, new endemics may appear. But while plants that are really very local may be completely killed out by a serious change of climate or other conditions, it is very unlikely that this will happen with plants that are already widely dispersed into a considerable variety of conditions. To imagine that a species that has become well adapted to certain conditions that occur in one country has become thereby *adapted* to those that may occur in some country widely separated from the first, is to press the idea of adaptation altogether beyond possibility.

TEST CASE XXVI. AGE AND AREA

There is no need to add much to the description already given in chap. III. One of its striking features is the proof that it gives that the distribution of a plant within a country, such as Ceylon or New Zealand, goes on the average with its total distribution outside that country. When one considers the differences in conditions that must exist, this goes to show that natural selection, in the sense of gradual structural adaptation, can have had little or nothing to do with the distribution. What kind of an "adaptation" can a species have acquired that enables it to go so far afield, into so great a variety of conditions? And still more difficult is it to explain why the species that are endemic in any given country are usually closely related to these species of large and widely ranging genera.

In Ceylon, for example, and the same can be said of other places, the species that are most widely dispersed locally, on the average, are those that range beyond the South Indian peninsula, i.e. beyond a line drawn from Bombay to Calcutta. The next most widely dispersed occur in Ceylon and in the peninsula only, while the least dispersed are the local or endemic species that do not occur outside Ceylon. All, of course, as pointed out in *Age and Area*, must be taken in averages, as an endemic in an old genus (in Ceylon) might be much older, and occupy more ground, than a newly arrived "wide", even if the latter also ranged to

tropical Africa or America. But on averages there are very great differences between the species of the three groups, and the statement above made as to relative distribution is fully borne out in all cases that have been investigated. Between the widely distributed species and the local endemics in New Zealand, there is a great difference in range (average length for wides 742 miles, for endemics 414).

On the theory of natural selection, it is quite impossible to make *any* prediction about what is likely to be found in studying the distribution of plants in such a place as Ceylon. The supporters of that theory tried to answer the author's attack by calling in two supplementary hypotheses, which as already shown (p. 24) are mutually contradictory. The Ceylon local species were supposed in the first to be local adaptations to the Ceylon conditions. But this did not get over the difficulty of the intermediate distribution of the species that also occurred in South India. Were they suited to the conditions that occurred in both countries, and if so what were those conditions, and how did natural selection adapt plants in such a way that some Ceylon things were confined to Ceylon, some reached as far as say Cochin in South India, while some got as far as Goa and some to Bombay? This overlapping of areas, which shows in all parts of the world, is a fatal objection to the theory of local adaptation as a general rule for the explanation of endemics, without something else to explain the varying distribution that they show. But in any case, it was a very remarkable thing that if they were really local adaptations to local conditions, they should be the rarest plants in those very conditions. Their general distribution was simply a reproduction on a smaller scale of the kind of distribution that might be seen in any big genus or family, or in the flora of any big country—all gave the same "hollow" curves. There was nothing peculiar about local endemism to distinguish it from any other type of distribution.

The rival supplementary hypothesis, which contradicts the first, and is the popular explanation at the present time, is that the endemics of a country are the relics of a previous vegetation. The tenacity with which this opinion is held, in spite of all evidence to the contrary, is really noteworthy, though a weakening is to be seen in the tendency to expand the idea of a relic. Such things as *Ceanothus* in North America may perhaps be brought into this category, though the genus has about forty species, which puts it very definitely into the large genera, but it does,

however, seem to belong to the vegetation that was largely destroyed there by the ice. But things like *Artocarpus*, with over sixty species, common in warm Asia, are now being called relics, because they have fossils in places not now occupied by them. But if these plants are to be counted relics, one might as well say that all widely distributed things, but probably not the local or endemic, are relics, for there are few widely distributed things that have not the possibility of fossils somewhere, for example the whole British flora that anywhere reaches the coast. There are rarely any fossils of the small and local genera that are usually called relics.

But the hypothesis of reliedom is no better than that of local adaptation in explaining the intermediate position of the Ceylon-South Indian things in the distribution. Are they half relics? No hypothesis other than that which we have termed age and area can explain the "hollow curve" into which all kinds of distribution fit. No theory involving natural selection or gradual adaptation can explain why 38 per cent of the genera of the world have only one species, 18 per cent two, and only 7 per cent three, and why the proportions are very much the same wherever one may go. There is no escape from these facts, and to say that they are accidental is simply to admit that the distribution of plants is largely accidental, and to ignore the rule under which they have probably come into being, the simple doubling of every species at intervals as time has gone on (cf. Yule, 75). The author has lately shown that the distribution of family surnames in the mountainous regions of Switzerland follows exactly the same rules as does the distribution of plants. No invocation of natural selection can explain why *Rochat*, which is a common name in its place of origin (the valley of Joux), should have spread more widely in the canton of Vaud than *Capt*, which is less common, or why the surnames should be arranged in "wheels within wheels" just like the species of the Ceylon or other floras. Nor can one invoke gradual adaptation to explain why in the far north-east of its range, *Rochat* is replaced by *Rojard*, which is much more easily explained by the general illiteracy of former days, and largely matches the way in which plant varieties occur. It will perhaps be well to quote part of the original note, by kind permission of the Linnean Society (and cf. fig. 6, p. 40).

*Surname-distribution of farmers
in Canton Vaud (Switzerland)*

As a sequel to Guppy's study of surname-distribution of farmers (who move about less than usual) in Britain, which showed a good "hollow curve" by counties, the author has studied Canton Vaud, which is about as large as Gloucestershire, but much broken up into more or less isolated valleys by mountains larger and smaller. Its nineteen "districts" average 64 square miles each, and they show as good a curve as, or even better than, that of the English counties. A very great number of the villages, especially in the more rugged districts, contain endemic names found nowhere else in the Canton. Not infrequently these occur on more than one farm, and then they usually show a curve just like that of plants, with the greatest number upon the smallest area (here one farm). The spread of a name may be due to various causes that can hardly be regarded as other than chance, as for example the chance that a farm may fall into the possession of a woman of family X. If she marry a man of family A, that family will rise in status by one farm, and X may even be extinguished. The same process happens with plants, and the plant (or the surname) that increases its numbers increases its chance of spreading. The bulk of the villages in the Canton have one or more names exceeding the rest in number, and in general these names show greater dispersal in the Canton (just as the commoner plants in Ceylon, for example, show greater dispersal outside the island). Spread is alike in the two cases, so that it becomes very difficult to call in adaptation or natural selection as the chief causal agent in distribution. Rochat, for example, is the commonest name in the valley of Joux, and has spread the most widely of the Joux names in the Canton. But there is no adaptation, nor any handle for natural selection, in the possession of Rochat as a name. No *single* plant, and no *single* owner of a name, of course, can become established anywhere without passing through the sieve of natural selection, but that is its chief action. The effect of selection upon a name, or upon a species, will be the sum of its effects upon the individuals, and one must remember the failures.

Age and Area is very strongly indeed in favour of differentiation.

TEST CASE XXVII. CONTOUR MAPS

It will commonly be found, in studying the distribution of the species of a genus, especially if it be of small or moderate size, that they are more densely congregated towards the centre of the distribution of the genus, and fall off gradually towards the

edges, so that when one draws a line round the outermost localities of each species one obtains a picture not unlike that which is called a contour map by the geographers, such as may be seen in any good guide-book to hilly country. If the genus be small, there will probably be only one generic centre, whilst the larger that it becomes, the more broken will the central part be, with more and more regions in which there is a concentration of species, like regions of the higher peaks in a geographical contour map. So long as a genus is of small or moderate size, the outermost or boundary species seems usually to be one species only, but as it grows larger it becomes rarer for there to be one species occupying the whole generic area, and one begins to find local concentrations of species in widely separated parts of the world, like that which is shown here in the map of New Zealand, with the species of *Ranunculus* there found. Here one finds three "wides" (as I have called the species which have a dispersal outside the country in question) occupying the whole area of the islands of New Zealand, and also reaching eastwards to the Chatham Islands, 375 miles away. Their distribution is thus by far larger than that of any other buttercups in New Zealand (fig. 9). The fourth wide has a distribution not very much less than that of the most widely dispersed endemic. The total length of the islands is 1080 miles and the breadth does not vary very much from 100 miles, so that the longitudinal range may be taken as a reasonable measure of the dispersal of a species. The endemics are evidently crowded together rather south of the middle of the South Island, whilst they fade out completely before the north end of the North Island is reached. Of the twenty-eight endemics, ten have a range not exceeding 60 miles of the length of New Zealand. If one take the ranges in differences of 200 miles—200, 400, etc.—one finds that fourteen, seven, five, one, one species have these ranges, or, in other words, the figures form the usual hollow curve of distribution, and this is shown by any New Zealand concentration of the larger genera. The general impression that one gains from a map like this is that the genus *Ranunculus* entered New Zealand probably from the south, and at some place in the southern half of the South Island, where the incoming species began giving rise to endemics, and on the average each species, wide or endemic, spread to the distance allowed by its age, and suitability to the conditions with which it met.

The same type of contour distribution is shown by the genera of a family, as fig. 10 shows. Incidentally, these contour maps

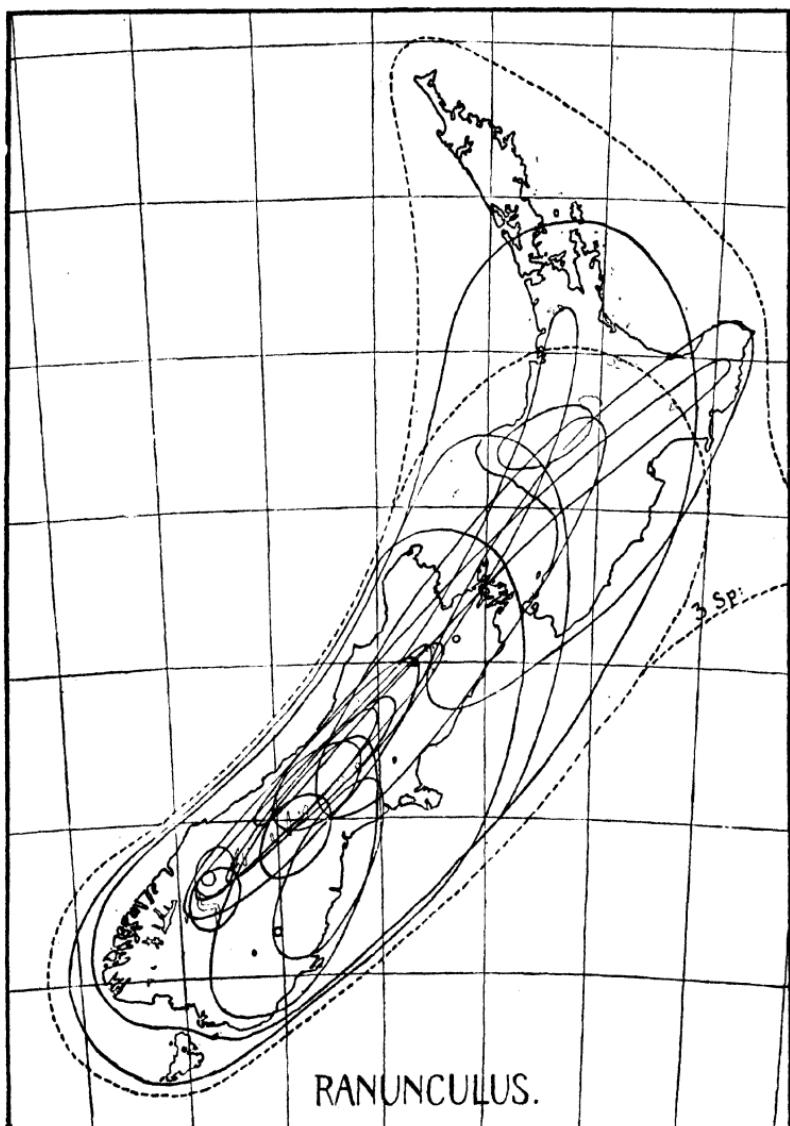
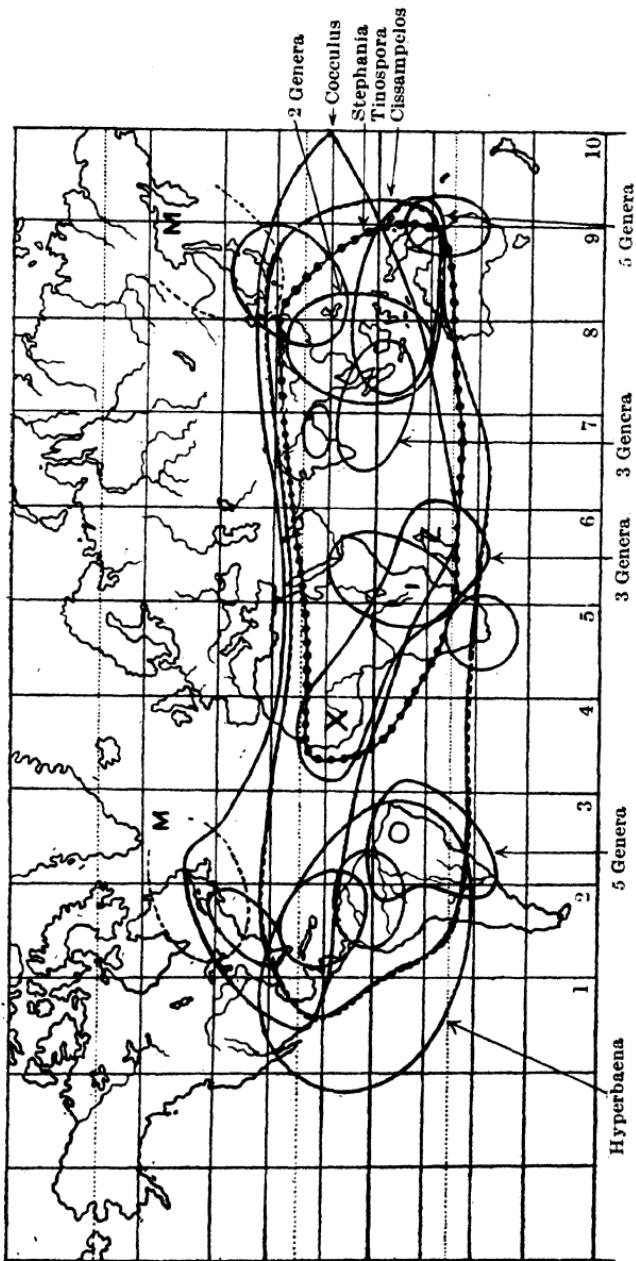


Fig. 9. Diagram showing the areas occupied by species of *Ranunculus* in New Zealand. Wides dotted; extension East includes Chathams.

(By courtesy of the Editor, *Annals of Botany*.)



Geographical Distribution of Menispermaceæ in outline.
 At X (West Africa) 12 genera. M = Menispermum.
 At Z (Madagascar) 5 genera.

(By courtesy of the Royal Society.)

Fig. 10.

show the absurdity of trying to draw a definite line of distinction between endemic and non-endemic.

Working upon the theories of Age and Area and of Differentiation, this distribution is exactly what one would expect to find, but it is extremely difficult to account for upon the theory of natural selection or of gradual adaptation. On that theory the widely dispersed things are supposed to be the best adapted. But to what? It is clear that if the distribution is very wide, each individual or group of individuals found in any small region *can* only be adapted to that region. Suitability to other regions that differed to some extent from the first could not be such an advantage to a species that it would help it to settle in the first region. Natural selection, picking out species suitable to A, would not at the same time pick out qualities that would suit the species to B; it could not even know, to put it in a kind of personal way, that B existed, and that A would gain in area of distribution by being able to settle there without further adaptation. A species must become adapted in turn to every change of conditions with which it may meet, whether differing soil, temperature, moisture, or biological conditions, and so on, and when at last it meets with conditions that go beyond its possible range of adaptation, then it will have met one of the boundaries that limit distribution, already fully enough described in *Age and Area*. Probably there is some kind of limit to adaptation (or it may be only to speed of adaptation) in most or all species. Sooner or later they will come up against a barrier, most often probably climatic, which they cannot pass. But at the meeting place of such barriers, e.g. in Ceylon at the junction of the dry with the wet zones, one not infrequently finds different species of the same genus, some on one side, some on the other. This is apt to suggest that at some time and place, one or the other species was becoming adapted to one or the other zone, and that some kind of turn of the kaleidoscope took place which resulted in the formation of the second species, better adapted to the new conditions, though its morphological differences probably had nothing to do with physiological problems, but were perhaps in some way a correlation.

The general evidence of contour maps, of which a very good example (*Beta*) may be found in *Nat. Pflanzenfamilien*, 2nd ed. vol. xvi c, 1934, p. 461, is entirely in favour of differentiation and age and area. It is sometimes suggested that at the centre of a contour map the conditions are more varied, but very little thought is required to show the absurdity of this contention. The

conditions in Britain are perhaps more varied than in any part of Europe, yet no genus has the centre of its map there, and several hundred genera have the one marginal species in Britain, and that only. If this conception were correct, the variety of conditions would tend to increase away from the sea. If one take family contours such as those shown in the map of Menispermaceae on p. 152, the case is even better marked. Such families as Umbelliferae or Cruciferae have their centres of aggregation well marked in the Eastern Mediterranean and Central Asia. But not only do they show there the maximum of species in general, but also the maximum number of monotypic genera with one species only. These are usually set down as relics, and why should relics be most numerous at headquarters? In their anxiety to prove the validity of natural selection people have worked upon more or less independent lines, which often clash badly with one another. Workers with floras of islands or of mountain chains have urged the conception of endemic species and monotypic genera as relics, regardless of the fact that other workers have shown that these relics are most abundant at the "headquarters" of the family, and are regarded as showing the great suitability of the family to that particular region.

A very difficult problem for supporters of the idea that conditions and their variety have anything to do with the contours is provided by their behaviour in New Zealand. The northern invasion of plants shows contours beginning in the north, with the last species of the genus somewhere in the south. The southern invasion begins in the south, and its contours fade away to the north, but each invasion passes over the centre of the other (where the conditions are supposed to be so varied) without taking the least notice of it. There cannot be conditions that only affect northern plants, or only southern, as the case may be.

TEST CASE XXVIII. TAXONOMIC RESEMBLANCES OF (GEOGRAPHICALLY) WIDELY SEPARATED PLANTS

This case has already been published, and the following description is largely quoted, by kind permission of the Linnean Society, from a paper in their *Proceedings* of 21 April 1938:

Whilst when first published both these conceptions—Differentiation and Young Beginners¹—were much opposed to current beliefs, there is no doubt that the latter, at any rate, is gaining

¹ I.e. the conception that the bulk of the very local endemic species, especially in warmer countries, are young species starting life.

ground, as may easily be seen by looking at various recent publications in systematic botany, where a great part of the endemic species are now admitted to be new. The first conception is also beginning to receive support. Systematists have in recent years made important additions to the evidence for mutational origin of species and genera, though themselves only trying to place these species and genera nearest to those which appear to be most closely related to them.

If one take as illustrations some of the more recent monographs in Engler's "Pflanzenreich", one notices at once the great geographical separations of closely allied species, genera, sub-families, families. In *Cardamine*, for example, species no. 70 is in New Zealand and Polynesia, no. 71 in the Azores, no. 72 in Chile. In *Euphorbia* one finds allied species in Venezuela and Cape Colony, in Persia and in Africa, in central Asia and in N. America, and so on. If in the Drabaeae (of Cruciferae) one join the consecutive related genera by a line, one crosses the Atlantic five times and the Pacific once, and usually goes well into the continent also. In the Arabideae the crossings are seven and six respectively, and in the Lepideae the whole map is covered with a web of lines.

Now with relationship like this, which is so much complicated by the great separations over the surface of the globe, to get an explanation by the method of accumulation of small differences is an extraordinarily difficult matter, and it is much simpler to call in the *linking genera* that cover the enormous gaps than to suppose that the related genera, say in Chile and Siberia for example, once overlapped or nearly overlapped each other, and that then destruction took place upon an enormous scale, and through all varieties of conditions and climates. All three of these subfamilies have various genera that cover the whole or much of the range, and it is much simpler to regard these as connecting links—as in fact the *ancestors*, directly or at times indirectly through intermediate genera, of the small scattered (though so often closely related) genera. One may take any view one pleases as to how they were derived from these large and widely distributed linking genera, though personally I hold to the views expressed in 1907, when pointing out how all the existing Dilleniaceae might have been derived, directly or indirectly, from *Tetracera*, the most widespread and about the simplest of the family. The only necessary thing is to get rid of the idea that small genera and species of restricted area are necessarily relics, and we have seen that this conception is now definitely losing ground.

If one suppose a genus to give off new species more or less in proportion to the area that it covers¹ (which again will be more or less in proportion to its age among its peers), it is clear

¹ For the mathematical consideration of the question, cf. Yule in *Phil. Trans. B*, 218, 1924, p. 21.

that all the offspring will carry a large proportion of the characters of the parent, and that therefore while offspring arising near together will be most likely closely to resemble one another, there is no reason why a close resemblance should not arise with a wide geographical separation.

It is rare to find a genus going far outside the limits of the genus that may be looked upon as the linking genus (e.g. *Draba* in Drabeae). When it does, one may imagine that in its "make-up" there was included a greater suitability to conditions that may be a barrier to the parent—it may be capable of growing in warmer (or colder), wetter (or drier), or otherwise different localities.

The author is not attempting to set up this "parent and child" theory as a universal rule, nor at present attempting to apply it to zoology; but there is no doubt that it will apply very well to most of the small families of plants, to a great number of the larger families, to a great number of the subdivisions of families, and to a great number of genera whose species behave as do those genera that we have been dealing with.

The theory of accumulation of small differences makes many of these and other phenomena very difficult to understand. To get two closely related genera or species so widely separated geographically by aid of the selection of small differences would be very difficult, for one would have to assume—if the differences be regarded as adaptational—that the conditions in the two places were very similar, though there is little evidence to that effect, or that the genera once touched one another in their distribution, and that there has been a vast amount of destruction. Not only so, but this destruction must have gone on through every variety of conditions to which the genera must have been adapted. There is *some* change and variety to be passed through between Greece and California, for example, or between Persia and Cape Colony, to take a couple of examples from the Lepideae.

It is probable that cytological study will throw some light upon this difficult problem and it is clear that what has been said here is fully in favour of the theory of differentiation, affording no support to that of natural selection.

TEST CASE XXIX. VARIETY OF CHARACTER WITH UNIFORM CONDITIONS

We have seen (p. 18) that the Podostemaceae and Tristichaceae, growing in the most uniform conditions that it is possible to imagine, yet show a very great variety of character and of structure. And not only so, but the characters are at times very definitely divergent, such things showing as bilocular and unilocular ovary, one stamen or two, many seeds or two to four, and

so on. There are about forty well-separated genera, with well-marked characters of flower and fruit, as well as strongly marked structural characters of the vegetative body. It is impossible to suppose that such structural characters as a bi- or uni-locular ovary can matter in the struggle for existence to a family like this, whose life is passed under water, the flowers only appearing a few days before their final death. The flowers in Asia, and to a considerable extent elsewhere, are fertilised by wind, so that their structural features are even less important to them than usual, though they mostly show the extreme of zygomorphism and stand rigidly vertical. The fruits produce a vast mass of seed, among which perhaps one in ten thousand may produce a new plant. The seeds have no adaptation for clinging to the rock, so that the survivors must be determined by chance.

A great many other families also show great variety in form though living in conditions that are comparatively uniform. Larger families are in general found to be living in a greater variety of conditions than small, but there are no general rules. But to co-ordinate the number and variety of the genera and species with the variety of the conditions was always an insoluble problem until it was shown that mere age had a great deal to do with it. With few exceptions, the older a family was, the greater the variety of conditions that it occupied, but there was no arithmetical relation between the two.

We may take a few examples of families and genera that show a considerable variety in themselves, without occupying a corresponding variety of conditions. *Pandanus*, which is found almost entirely in the uniform conditions of seashores or marshes, has 180 species. The Naiadaceae (1 genus with 35 species) and the Aponogetonaceae (1/25) are water-plants of very uniform conditions. The Cyperaceae, mostly in swamps or in sandy places, both of which must be very uniform, show 85/2600. The Bromeliaceae, epiphytic or on rocks, and therefore in very uniform conditions, are 65/850, the Juncaceae, in damp and cold places, 8/300. The orchids, largely epiphytic, where the conditions must be very uniform, are 450/7500. The Salicaceae, mostly mesophytic trees, are 2/180, the Loranthaceae, woody semi-parasites, are 30/520. The Balanophoraceae, internal parasites, whose conditions must be *very* uniform, show 15/40, and *Orobanche*, a semi-parasite, has 90 species. The halophytic Chenopodiaceae have 75/500, the xerophytic Aizoaceae 20/650, the water-inhabiting Nymphaeaceae 8/50, the insectivorous marsh-loving *Drosera* has 90 species.

Nepenthes has 60, all living in very much the same conditions. *Begonia*, mostly in the undergrowth of damp forests, has 750, the xerophytic Crassulaceae 25/1500. *Impatiens*, mostly in the mountain flora of India and Ceylon, has 350 species. There are six species of *Sonneratia*, all mangroves, whose conditions of life must be the same. And so on. From these one can work downwards through smaller and smaller families, showing less and less variety, down to single species like *Hippuris vulgaris* of family rank. The smaller the family, on the average, the smaller is the area that it occupies (size and space, p. 113 of *Age and Area*).

Perhaps the most striking example of a great number of species all occupying practically identical conditions is the existence of the great group of the Fungi, more especially those that are internal parasites, where the conditions must be exactly the same, except for the chemical differences in the sap of one host and of another, differences which must be discontinuous, as the different chemical substances that occur are discontinuous. The eight genera *Clavaria*, *Fomes*, *Marasmius*, *Mucor*, *Penicillium*, *Peronospora*, *Puccinia* and *Saccharomyces*, all living in extremely uniform conditions, have 2500 species among them.

As in related forms the number of species goes up with the age and distribution of the genus or family, it is much simpler to look upon it as going simply with the age—the larger genus or family, with the larger distribution, is the older. If the conditions also become more varied with increasing age of the family, as they almost always do, this probably helps to increase the number of species by the stimulus that it gives. There is nothing to be extracted from the figures that will go to show that natural selection, or variety of conditions, is responsible for the numbers of forms that exist. Probably as time goes on, and at any rate if there is any stimulus, evolution has to go on.

TEST CASE XXX. A COMMON TYPE OF DISTRIBUTION IN INDIA AND ELSEWHERE

A proposition very difficult of explanation is put before the supporters of natural selection by what is a very common type of distribution, long ago pointed out by Dr Guppy in the islands of Polynesia, and by the writer in India, Ceylon, and elsewhere. This is the polymorphous widely ranging species, accompanied by few or many species confined each to one part only of its range, and endemic to the regions that they occupy. Guppy noted three stages in the development of local endemism. First, the

island was occupied, so far as a given genus was concerned, by one or more widely ranging species, usually very variable, such for example as *Metrosideros polymorpha*. Then the wide-ranger was accompanied by one or more local endemics, allied to it, and finally there were only the endemics. He thought that the wide-ranger had given rise to the endemics, and might, or even did, ultimately disappear (swamped, cf. 66, p. 95) (cf. 74, pp. 611–13).

It is the general experience of systematists that it is only in numerous and widely ranging forms that this variability occurs (cf. p. 132 for axioms). Linnaeus (12th ed., II, 324) gives a list of thirty such polymorphous genera, including willow and saxifrage in Europe, oak and Aster in North America, Cactus in South America, heather and everlasting at the Cape.

Another way to bring out this point is to look at the synonyms in generic indices like the *Index Kewensis*. The first forty-five generic synonyms at the beginning of C are referred to genera of an average size of 94, the mean for all genera being 14–15. The first seventy in de Dalla Torre's *Index* are merged in genera with an average of 70, or in both cases definitely *large* genera.

Let us begin with the Indian *Anemones*, which show

<i>A. rivularis</i>	All mountains of India and Ceylon
<i>rupicola</i>	Kashmir to Sikkim
<i>vitifolia</i>	Himalaya, Mishmi Hills
<i>Griffithii</i>	Sikkim, Bhotan, Mishmi
<i>Falconeri</i>	W. temperate Himalaya
<i>obtusiloba</i>	Temp. and alpine, Kashmir to Sikkim
<i>rupestris</i>	Alpine, Kashmir to Sikkim
<i>trullifolia</i>	Sikkim to Bhotan
<i>demissa</i>	Alpine, Sikkim
<i>polyanthes</i>	Kashmir to Sikkim
<i>tetrasepala</i>	Western Himalaya
<i>elongata</i>	Garhwal, Nepal, Khasias

Or take Clematis, § Cheiopsis; *C. montana* is common all along the Himalaya, while *C. napaulensis*, *C. barbellata* and *C. acutangula* are confined to particular sections. These two genera are simply the first that occur in the flora, and almost any Himalayan genus will show the same thing, whilst it is also shown by the genera of lower levels, e.g. *Portulaca*:

<i>P. oleracea</i>	All India and Ceylon, and all warm countries
<i>quadrifida</i>	All India and Ceylon, and palaeotropical
<i>Wightiana</i>	Carnatic to Ceylon. Endemic
<i>tuberosa</i>	Behar to Ceylon. Endemic
<i>suffruticosa</i>	W. Peninsula, Ceylon. Endemic

Other genera, e.g. *Amoora*, *Celastrus*, *Hippocratea*, *Leea*, *Limacia*, *Olax*, *Salacia*, *Tinospora*, *Zizyphus*, from the first volume of Hooker's *Flora*, show the same thing. Clarke (4) says that in the Himalaya closely allied species of *Didymocarpus* are confined to single districts, though there appears no reason in soil or climate why they should not spread to adjoining valleys.

Now to explain such phenomena as these by aid of natural selection is very difficult. The range of the wide-ranging *Anemone*, for example, is put down to its "adaptation", though to what exactly it is adapted is not explained. If it suit (as it does, place by place) the very varied range of conditions in which it is found that must be due to functional or physiological adaptation as it moved from one region to another. We have no evidence that a seed from say Ceylon would at once suit a station in the north-west Himalaya, without first acquiring the necessary local adaptation which it would have received as a matter of course had it been slowly transported from place to place by nature's method. But it would then, in all probability, cease to be fully suited to the Ceylon habitat. But why should it be accompanied by eleven local species? All these are endemic to their own regions. In their anxiety to disprove my contention that such local endemics are young species as compared with the wide-rangers, my opponents have gradually pinned their faith to relicdom. But why should *A. rivularis* leave eleven defeated relics in its range of distribution? It looks as if selection had been very strenuous, and was greatly diminishing the number of species, not increasing it (p. 90). There is absolutely nothing to prove that any of them are relics, and no feature in *A. rivularis* that gives even a faint suggestion that it may be adaptationally superior. It covers all the mountains of India and Ceylon, and why are there no local relics in any of the southern mountains? None occur south of the Khasias. But there can be little doubt that *Anemone* advanced from north to south in the Indian region, reaching Ceylon last of all, so that it would be younger in the south than in the north. By the theory of age and area, its peculiarities are at once explained. *A. rivularis* arrived first somewhere in the Himalaya, where only the local endemics are to be found, and it has not been long enough in the southern mountains to mutate off new endemics there. The relic explanation is altogether too fanciful to be accepted, as is also that of local adaptation, which also will not explain the crowding together of the endemics in the north. Nothing hitherto proposed with the exception of age and area

is capable of explaining problems like these, which occur in hundreds and all closely similar. Natural selection is completely incompetent to do so. What Anemone shows in the Indian region is a contour map, which we have already shown on p. 149 to be completely favourable to differentiation and to age and area.

TEST CASE XXXI. LARGE GENERA THE MOST "SUCCESSFUL"

One cannot accept the large genera as the most successful in the light-hearted way in which this has been done under natural selection. They are not usually composed of numbers of widely distributed species—their successes are limited to comparatively very few. We have seen above how few of the numerous *Siparunas* or *Mollinedias* are widely distributed, and yet these are by far the largest genera in their family. And the same phenomenon is almost universal. If we take as another example the Styraceae, of which the monograph is lying beside me, we find a family of six genera, four with three species each, one with two, and *Styrax* itself with 100. Here surely is a family with one conspicuously successful genus. But when we look at the whole distribution, there are only four widely dispersed species in the whole family, one in *Pterostyrax* and three in *Styrax*. The distinction between these genera is mainly that one has a superior, the other an inferior, ovary. Upon the hypothesis of natural selection, therefore, the family consists of about four successful species and 110 relict species. And not only so, but the *Styrax* that is by far the most widely dispersed has a very discontinuous distribution (W. As., Eur.; W.N.Am.), a thing that does not occur with the small genera, usually looked upon as relict species. It is much simpler to regard the widely distributed species as older, the local as younger, as differentiation requires.

TEST CASE XXXII. CHARACTERS MORE CONSTANT THE MORE USEFUL

This is sometimes advanced as a corollary of the theory of natural selection, and indeed it seems almost necessarily to follow. How much substance there is in the argument, however, may be judged from the fact that the most constant characters in plants are notoriously those that are the most important in the classification (for the obvious reason that they are the most constant). But the higher one goes in the classificatory characters, from those of species to those of families, the more constant do

the characters become, and the less functional value do they have, as is universally admitted. This test is entirely against natural selection, even if it do not specially favour differentiation.

TEST CASE XXXIII. RELATION OF MONOCOTYLEDONS TO DICOTYLEDONS

A feature in geographical distribution to which Hooker called attention in 1888, and which was never explained until *Age and Area* gave the key to it, is described in the following quotation (18): "The conditions which have resulted in Monocotyledons retaining their numerical position of one to four or thereabouts of Dicotyledons in the globe and in all large areas thereof are, in the present state of science, inscrutable." The exactness of the relation is remarkable. The latest figures in the writer's possession add up to 36,639 species of Monocotyledons and 145,718 of Dicotyledons, or almost exactly one to four.

So long as one keep to large areas, and to the centre of the land masses, the relation keeps wonderfully steady, but when one comes to the edges of vegetation, especially to the north or to the south, one finds fluctuation beginning, as also in the tropical belt from Malaya (which has 26 per cent of Monocotyledons) through Ceylon (27 per cent). While the average proportion is just 20 per cent, and in the Kermadec Islands north of New Zealand is 21 per cent, it is 31 per cent in the Chatham Islands to the east of New Zealand, and 45 per cent in the Aucklands to the south, and again 26 per cent in Juan Fernandez and 30 per cent in Tasmania, all these figures suggesting that the old southern continent was a great home of Monocotyledons. In Europe there is a belt of high proportion of Monocotyledons from Sardinia through France and Britain to Iceland. In the Canaries the proportion is only 15 per cent.

Now there is no "monocotyledonous" mode of life to which this group can have been adapted. Every kind of life is represented, and there is nothing in common in mode of life between such things as orchids, grasses, lilies, aloes, bulrushes, watersoldiers, palms, aroids, duckweeds, rushes, Bromeliads, yams, bananas, gingers, etc. The steadiness of the proportion of Monocotyledons to Dicotyledons goes to show that in their dispersal adaptation played but a small part, and that it was primarily governed by the laws of age and area, as is demanded by the theory of differentiation.

**TEST CASE XXXIV. OVERLAP OF LARGEST
GENERA IN A FAMILY**

If the differentiation explanation of the origin of a family be the correct one, the first two genera of a family, the largest upon the whole, should overlap in their distribution, as one of them sprang from the other, but there is no reason why this should be so under natural selection. Geological or other changes may, of course, at times have rendered this impossible. Upon examination, we find that in the majority of families this overlap does occur, though there are a number of families like the Apocynaceae with a large genus in each of the continents, or in the Old and New Worlds. Exceptions are frequent among the families of the southern hemisphere, with their broken areas of distribution, but in the greater number of families the rule holds. Among the small genera in a large family, this is rarely the case, but in a small family it usually occurs. It is not impossible for a grouping like this to have been produced by natural selection, but there must have been something upon which it could get a grip, and one can scarcely ever find anything of this kind.

CHAPTER XIV

GENERAL DISCUSSION

THE results to which this work leads being somewhat subversive of current opinions, it will be well, perhaps, briefly to restate parts of the argument in other words. Some of it appeared eighteen years ago in *Age and Area*, but the propositions there put forward were not accepted, though the arguments brought up against them appeared to the writer to be lacking in logical force, and he has remained faithful to his published opinions. Bateson alone among reviewers realised that the discovery of the "hollow curves" was one of importance, and the only thing that opponents have been able to bring up against them is that they are "accidental", just as the curve of names from the telephone book, or of the names in Canton Vaud (p. 35) is "accidental", which is exactly what the writer was out to prove.

Until some eighty years ago, the appearance of the vast numbers of forms of life that people the world, and that are usually known as the species of animals or plants, was put down to a somewhat crude intervention of the Supreme Power, which was supposed to have created all the hundreds of thousands of them, each species in its existing form, and to have placed each in a more or less definite region, where it is still commonly to be found (p. 2). When studied in more detail, however, many difficulties cropped up, difficulties that became ever more insistent, and that at last resulted in the sweeping away of the old theory of special creation, then the background of biological work. One great difficulty, for example, was to explain the evident likenesses that one may see in the tiger, the leopard, and the cat, or the daisy and the sunflower, resemblances so great that they seemed to point to definite relationship, as indeed had been suspected since the days of Aristotle.

In 1859, with the appearance of the *Origin of Species*, there began the long reign of "Darwinism", lasting to the present time. Darwin's immortal service to science was to establish the theory of evolution—that every living species has been derived from some other by direct descent, accompanied by such modification that for example the tiger, the leopard, and the cat might all be derived from a common parent sufficiently far back. Unfortunately the name of Darwinism was popularly given rather to the

mechanism by which these changes were to be effected, i.e. to the struggle for existence that was a familiar everyday experience, allowing those gifted by nature or by parents, or by chance, to succeed, while the non-gifted usually failed. As every living being tends to produce more offspring than there is room for, some must obviously be picked out, and this selection, or "survival of the fittest", Darwin called natural selection. Being so familiar, it had a great psychological appeal, and was soon taken up in all directions. It was evidently an almost complete reversal of special creation; instead of being created, beings were evolved, and instead of being discontinuous, the process was continuous.

Picking out only variations that gave some advantage, natural selection worked by what we may call gradual adaptation (p. 4), which was an essential feature of the theory. But it is clear that a small improvement in adaptation would not be enough to create a new species, which is usually more or less sterile with its near relatives (a functional difference), and shows various structural differences as well. It had to be assumed, therefore, that the process would go on until the line of mutual sterility had been passed, and the differences had become great enough to mark it as a new species. It was the structural differences that showed that there had been any evolution at all, and so it had to be assumed also that they were adaptational, marking the adaptational advantages that had accrued to the organism. Functional adaptation was ignored, though the morphologists had long insisted that structure had little or nothing necessarily to do with function.

The freedom of the position of natural selection was really lost very early in its history, when Darwin had to give way to the criticism of a well-known professor of engineering, Fleeming Jenkin, who pointed out that unless a great many individuals varied in the same direction over the whole of a considerable area, the improvement would promptly be lost by crossing. Darwin therefore stipulated for such a beginning, which seems only likely to happen under the action of some external force, and which practically excludes the action of biological factors, which are usually local. Improvement seemed unlikely in the fluctuating variation upon which Darwin usually relied, for some might go up when others went down, and crossing would level them. This criticism took much of the spring out of the action of natural selection, for instead of remaining a simple affair of individuals,

as it was in daily life, it was assumed to be a competition of groups. Whatever may be the case with animals, there seems little or no reason to imagine that plants compete as groups. It is this assumption which has become so marked a feature in social and political life—that the best, and incidentally the most satisfactory, solution of a difficulty or of a competition lies in the conquest and dominance, or even in the extermination, of the opponent. Species, to begin with, are not structural units with all individuals just alike, any more than are language groups of mankind. The nearest approach to this condition is in such cases as *Coleus elongatus* (p. 24), a well-marked "Linnean" species where there are so few individuals—perhaps a dozen in this case—that they do not allow of a great range of variation. There is also less range in the small "Jordanian" species, but these, on the theory of differentiation, are later phases in evolution than are the Linnean species. As one of the latter increases in number, and in occupied area, from its first beginning, and thus probably comes into greater variety of conditions, and into more crossing with other individuals, the more variation does it show, on the whole (p. 159).

The following quotation shows the point of view that is being taken up as the result of the work of agricultural geneticists: "Studies of crop populations have shown that natural selection does not result in the survival of the fittest *type*, but of the fittest *population*, and the fittest population is almost always a mixture of many types" (78). This agrees with the ordinary observation of everyday life, that natural selection is individual in its action.

The plants (or group, occupying the whole of the locality) that did not show the useful improvement (or another as good) were killed out in the struggle for existence, that also killed out the parent, which was assumed not to become adapted.

It is clear that there are many weak points in the Darwinian position, and to support them all kinds of assumptions and supplementary hypotheses have been brought up. But there has never been any good proof (1) that evolution proceeded essentially by improvement in adaptation, (2) that it was gradual and closely continuous, (3) that the phenomena of the structure of plants reflect the adaptation that has gone on in them, or (4) that groups of plants can compete as units.

When one comes to look into the matter, one soon realises that the theory of natural selection rests upon a great many assumptions, sometimes backed by more or less proof, sometimes not.

Yet I have been assured by one of its most eminent supporters that it contains none, but rests upon proved facts. The following list gives the most important assumptions:

1. That a small *structural* variation may be advantageous enough to call in the action of natural selection (pp. 4, 13).
2. That a small advantageous variation may be inherited (p. 4).
3. That it may be added to, and become more and more marked in succeeding generations (pp. 4, 54, 106, 165).
4. That the whole number of individuals upon a considerable area will show the same advantageous variation, i.e. probably.
5. That the variations are controlled by external conditions (pp. 5, 165).
6. That the whole number of individuals carrying a useful variation can, and does, fight as a unit (pp. 107, 142, 144, 166).
7. That the parent form does not also become adapted (pp. 4, 13, 54).
8. That adaptation is structural rather than functional (p. 4).
9. That structural characters are the means of expression of adaptation (p. 14).
10. That differences in structure mean differences in adaptation (pp. 52, 109).
11. That the variety with the advantageous variation, slight though it would be at first, will defeat the parent in the struggle for existence (p. 4).
12. That the new form produced by natural selection, and adapted to area B, became thereby also better adapted to A, the area occupied by the less well adapted parent species (p. 144).
13. That all variations that survive must be useful, or must be correlated with variations that are useful or at least that are not harmful enough to be of serious disadvantage (pp. 57, 58).
14. That the new form will invade the territory of the old, and kill it out there, without being lost in hybrids (p. 143).
15. That the defeated species will gradually become relics, and ultimately disappear (pp. 4, 17, 91, 97-8).
16. That fluctuating variation is irreversible.
17. That fluctuating variation is qualitative as well as quantitative.
18. That fluctuating, or even small, variations can be added up so that they pass the sterility line that usually divides one species from the next.

19. That the needful variations will appear at all (p. 55).
20. That natural selection can act continuously upon them (p. 54).
21. That most or all of the individuals that do not show the favourable variation will be killed out (p. 54).
22. That conditions will continue to vary in the same direction long enough to enable the sterility line to be passed (pp. 54, 55).
23. That natural selection is so strenuous in its action that the sterility line *will* be passed (p. 55).
24. That when a species has become well started upon a variation in one direction, there will not be offered to it one in another direction, obviously better (pp. 55, 109).
25. That the adoption of one variation does not interfere with the adoption of another (pp. 55, 109).
26. That when one variation has done its work, it shall be followed by another of those that mark the species (p. 55).
27. That morphological and anatomical necessities override the effects of natural selection (p. 110).
28. That economic botany is of no importance from the point of view of natural selection (p. 8).
29. That advantageous structural variations are so desirable that they will commonly be followed up to a result of 100 per cent (p. 114).
30. That natural selection will produce uniformity in structure of a morphological feature (pp. 55, 114, 124).
31. That there was some reason why transitions were dropped out more and more as evolution went up towards families (p. 113).
32. That varieties are incipient species, species incipient genera.
33. That numbers would increase greatly under selection (p. 90).

This is a very formidable list, and a mere glance will show that many or even most of the assumptions still remain such, though by the adoption of mutation in place of gradual variation several of them have been removed. It is, therefore, clear that the theory of evolution by the agency of natural selection, picking out gradual improvements in adaptation, chiefly structural, is still a very long way from being established, and as no evidence has been found in seventy-five years to prove many or most of the assumptions, one may be permitted to feel somewhat sceptical of its discovery. Evolution is now thoroughly well established, and whether natural selection carried it on or not is a matter of indifference to it.

The theory of natural selection, holding as it did that everything was gradually acquired, went to show that evolution must be gradual and continuous from one structure to its successor of different form, and this soon led to difficulty. The facts of economic botany (pp. 8, 89) among others, though dismissed as unimportant since they did not favour natural selection, showed that there was much discontinuity in evolution, and Bateson's work (1) showed the same thing.

The continuous small fluctuating (infinitesimal) variations upon which Darwin chiefly relied were not fully hereditary (p. 10); they were not differentiating, but simply up and down in the same character, nor were they irreversible; and they could not be accumulated beyond a certain point (p. 10). They could all but never be found to show adaptation, whilst the differences became more and more marked, and less and less adaptational the higher that one went from species to family, this illustrating the principle that we have termed the divergence of variation (p. 74). Species, again, usually showed several points of difference which were unconnected with one another so far as anyone could see, and it was very hard to see how selection could deal with so many. Species also proved to be mostly local in the big or "successful" genera, so that their adaptation must have been generic, and it was very hard to understand how this could have been the case. If it were so, natural selection, working upwards from the species, could hardly explain it. If all specific characters were correlated, then the greater portion of evolution did not show the effects of natural selection (p. 11). It was almost impossible to see how gradual selection could pass the rough and ready line of distinction between species, the fact that they are almost always more or less mutually sterile. No transition stages, again, were to be found among the fossils, though one would have expected to find such upon a theory that was based upon the separation of genera and families, to say nothing of species, by the continual destruction of transitional forms on account of their inferiority to the more perfect. Nor could one find among the fossils any indication of the gradual formation of existing families, etc. These seem to appear already fully developed, and in widely separated sections of the classification of flowering plants.

Evolution could only go on if the right variations were to appear; natural selection would kill out any that were harmful, and would be indifferent to any that showed neither value nor

the reverse. Also evolution could only go on provided that natural selection could act as desired, another assumption. Then the freedom of action of selection was destroyed by Fleeming Jenkin's criticism, though the fact was hardly realised. Finally, selection proved itself incapable of explaining many of the facts of geographical distribution, a subject which is completely bound up with evolution.

Immense effort was put into the study of adaptation fifty to sixty years ago (p. 52), but with little or no result other than to show that no one in his wildest dreams could attach adaptational value to the bulk of the structural characters that distinguish one plant from another, and show that evolution has really gone on. There was also no doubt that what little adaptation did show decreased rapidly as one went up the scale above the rank of genus; but the higher divisions were supposed to be made by the killing out of transitions, which would imply that selection came more and more into play to make larger and larger divisions. The facts, when judged in the light of the theory of natural selection, are evidently somewhat incompatible.

Early in this century de Vries brought in the theory of mutation or sudden change, which in many respects got over the worst difficulties of Darwinism, and would have surmounted more had not people taken up a somewhat illogical attitude with regard to it. It was admitted that small mutations could take place, but people were averse to admitting large ones, for that would probably remove *any* effect of natural selection in guiding evolution. It would be almost absurd to suppose that it showed its work by the production of large and sudden differences, though it is not impossible, for one may imagine it perhaps selecting slight genic changes, and these being added up till the strain in the nucleus produced some kind of kaleidoscopic effect by a readjustment. The writer suggested in 1907 that "a group of allied species represents so many more or less stable positions of equilibrium in cell division" (70). But though by the adoption of small mutations the power as a determinant of evolution was taken away from natural selection, so that it could no longer start the improved adaptations, it was expected to carry them on and to increase them, gradually or by further mutation. Of course it would only carry on those which had, so to speak, passed through its sieve, and had proved to be of definite value. We were still, however, without any indication that the characters produced in the small mutation had any adaptational value, so that their survival would usually be due simply to the fact that natural

selection was indifferent to them. But if this were so, it could not carry them further. This being so, why not go the whole course at one effort, and admit that selection had little, or perhaps even nothing, to do with the *evolution* of the organisms that now exist in the world, however much it may have improved them after their evolution, or fitted them to the local conditions in which they were trying to live? Everything, before it can become established, must pass through the sieve of natural selection, and each new individual, in any place, must do the same, but the characters of that new species or individual were not *selected* by it. If selection does not begin a species or an individual, it has no responsibility for its arrival, but it will kill it out if it be unsuitable to the conditions of the place in which it appears, at the time at which it appears. Why then should natural selection be needed at all for structural change, if it does not begin it, and when one can generally find no adaptational value in it?

This is very much the position that the author took up in 1907, basing his change of view more or less upon this line of reasoning, and admitting that no mutation that may be needed for the purpose in view—the formation of species, genera, or families—is too large for possibility. There is little or no evidence that structural differences in root, stem, leaf, flower, fruit, seed, have any adaptational value, yet it is these things that make up the characteristic differences that separate one species, genus, or family from another (cf. *Thalictrum*, etc., on p. 104, and lists in Appendices). There is no evidence that climbing plants (p. 57) have gained by the fact that they can climb. The same genus sometimes contains both climbers and non-climbers, and the former must have erect plants upon which to climb, with few exceptions. Supposing that they smothered all the erect plants by their success, as they might very easily do if really "successful", both they and the latter would be in a bad way, yet there is nothing to prevent it.

The view that mutations are necessarily small rests to some extent upon the opinion that a Linnean species is composed of a great assemblage of micro-species which breed true. But it can only be so if it consist of a great number of individuals and occupy a large area. Upon the theory of age and area, as well as upon that of differentiation, this means that it is older than the small and local (allied) species, which is so often Linnean in the sense of marked difference, but cannot show great variety through lack of numbers (p. 182).

We imagine, then (under the theory of differentiation or diver-

gent mutation), that families, genera, and species may any of them be the result of a *single mutation*, more divergent in genera than in species, in families than in genera. These ideas receive great confirmation in the actual structural differences that separate plants. As one goes up the scale from species to family, the divergence of the characters of separation increases upon the whole, as is at once shown by any good dichotomous key. A feature of special interest is that the divergences become more and more such as allow of no intermediates or transitions at all, as for example, a berry and a drupe, an achene and a follicle, an anther with slits and one with pores. But if this be the case, the character, one or the other of a divergent pair, must have appeared at one step, so that, so far as one can see, natural selection can have had no hand in its appearance. The higher that one goes in the direction of the family, the less adaptational value can one find in the characters, so that the less is the handle that is offered to natural selection. Competition is greatest among individuals, less among species, still less among genera, and so on upwards. Yet the distinctions become greater along the same route, and the puzzling question is put as to how the diminished competition can bring about the larger and more permanent distinctions. Why also are these characters of so slight (if any) functional use? If natural selection be the active agent in evolution, it must have been working at its highest pressure among the highest groups to separate them as they are separated, and also must have been working all the time to pick out characters with greater adaptational value; whereas in fact one finds the characters to be of less and less value as one goes upwards in the supposed track of natural selection. In seventy-five years no one has been able to prove any functional value for them. The uniformity of the statistics of the various continents and other large areas (66, p. 180) in the proportions of genera of various sizes, in their distribution, in the relative sizes of families and genera, etc., shows that one area is just like another, and that evolution must be going on in the same orderly way in all.

Though going to Ceylon an enthusiastic supporter of natural selection, the author found it needful to change his views after some years of tropical experience, both in the forest, and as the result of a minute study of the Podostemaceae (p. 18). Though at first glance looking as if they showed great adaptational differences, these plants all live under the most amazingly uniform

conditions, with nothing special to which to be specifically adapted. The life in moving water, and the loss of proper polarity of the plant (p. 20), are common to all. Yet there are about forty genera with many species. The most reasonable explanation is that evolution must go on, with or without adaptational reason, and is not necessarily a matter of local adaptation. All are compelled to "adapt" themselves more or less to the action of the permanent force that acts upon them, which cannot be escaped in any way.

The author's work with endemic plants, which has occupied many years, also showed that the old (and still more or less current) view, that they are relics of previous vegetation, had no sound basis. Under the Darwinian theory, there had to be found somewhere some at least of the species that had been defeated in the struggle for existence and were dying out. The harmless endemics just came in conveniently to fill this position, but while there are undoubtedly many relics in regions that were cooled in the glacial periods, one cannot suppose this of most of the local species of warmer climates.

As one result of this work, the writer discovered the "hollow curve" of distribution (chap. IV) that shows in plants and animals, and in many other cases, such as surnames, and even in inanimate objects (cf. p. 35). It shows well in areal distribution, many species of any genus occurring on small areas, few on large. It shows still better in the distribution of the genera in a family by the numbers of species that they contain. On the average, from which there is but small variation, with reasonable numbers, about 38 per cent of genera have only one species, 12 per cent two, and 7 per cent three. The curve turns the corner between three and five, and tapers away in a long tail, and the larger the family the more accurately does it follow the curve. When plotted, as $38 + 7$ make more than twice twelve, the curve has the dip in the middle that gives it its name (fig. on p. 86). When plotted in logarithms, the curves form close approximations to straight lines, showing that all have the same mathematical form, and have appeared as the result of the same law, working upon all. The mathematical treatment of the subject will be found in Yule's paper (75), the introduction to which should be read by all interested in evolution. The general law, as he showed, that immediately governed it was that at the end of certain intervals, probably very variable in length, *a genus became two, and both, as a rule, survived*. The parent genus of the two was not neces-

sarily killed out, as was the rule under natural selection. In fact, as the curves must be the result of uniform pressure, they could not result from, or under, natural selection.

The logarithmic curve undoubtedly shows some marked deviations from the straight line at the further end (cf. p. 87), and Longley (25) says "the hollow curve, we may therefore reasonably assume, results from some sort of compounding of a series of geometric series of different common ratio, but all lying between the limits of $\frac{1}{2}$ and 1".

But if genera and species are formed like this, it must almost certainly have been by single steps, and if the old ones were not killed out, natural selection can have had little or no influence in the matter. They cannot have been formed by structural adaptation. Gradual mutational change is no more satisfactory than the gradual changes that were supposed to have been effected by natural selection, for in the vast majority of cases where such small changes have been seen, there has been no possibility of imputing to them any functional value whatever. On the Darwinian theory, where the parent is killed out, it is very hard indeed to see how there can have been any increase in numbers (Test case i, p. 90).

One great advantage of the large mutations for the formation of species, and still more of genera and families, that are demanded by the theory of differentiation, is that at one step they will cross the "sterility line", the rough and ready distinction that separates a species from its nearest relative. The new form will at once become *isolated* (chap. VII), and there will be little likelihood of its being lost by crossing. As we have seen, isolation may be of very great importance in the establishment of new species, if not also in their evolution.

When one considers the fact (pp. 132-4) that the more primitive things are more widely distributed, that a genus (unless monotypic) occupies a wider area than at any rate all but one of its species, and again that there is no evidence to show that there is any adaptational reason why a small variety should become a larger one, or the latter a species, a species lead to a genus, and so on, it would seem, as it seemed to (the late) Dr Guppy and to the writer over thirty years ago, that we have been to a large extent trying to make evolution work *backwards*. It was infinitely simpler to work forwards *throughout* evolution, beginning always with the family, deriving the genus from that, the species from the genus, and the variety from the species. In fact, with

the absence of adaptational reasons for progress, and with the frequent impossibility of transitions (especially in the characters of the higher groups) it seemed to be almost the only way.

My friend Dr H. B. Guppy was perhaps the first to call proper attention to the fact that the Darwinian theory was trying to work evolution backwards. He says (12): "It follows from the foregoing remarks that no plant groups, in the sense of the great orders, could have been produced on the evolutionary lines implied in the Darwinian theory" (i.e. beginning with small varieties and going through species to genera and families), and continues "to lay down, as the Darwinian evolutionist does, that the order of development begins with the variety...species...genera...families, is to reverse the method followed in nature, since it implies that the simpler, least mutable, and less adaptive characters that distinguish the great families are the last developed. This could never have been. Nature has ever worked from the simple to the complex, from the general to the particular. Had she followed the lines laid down by the Darwinian school of evolutionists, there would be no systematic botany. All would be confusion. There would be no distribution in the sense in which the term is generally understood, and the plant world would be a world of oddities and monstrosities."

It is upon such propositions and facts that the pre-Darwinian theory of differentiation or divergent mutation is now founded. Natural selection is no longer to be regarded as the mechanism of evolution; it does not choose what shall be evolved, but it decides in each case, individually, what shall be allowed to live. Probably the bulk of the structural characters make little or no difference one way or the other, and so are indifferent to natural selection. Evolution ceases to be a mere matter of chance, and comes into that scheme of things of which Jeans has said that all the pictures which science draws of it are mathematical pictures. What causes it to go on we have yet to discover, but we can make one important step by finding out in which direction evolution moved, for that involved in the theory of differentiation is the exact opposite of that involved by natural selection. One goes from the family downwards, the other from the variety up, and as there is as yet no evidence to show that it moved in one particular direction, we are free to take that for which there is the better evidence.

After fifty years of work, the author has come to the conclusion that *evolution and natural selection work at right angles to one*

another, with but slight mutual interference, the latter being quite possibly greater in animals. The evolution *provides* the structurally different forms of life, while natural selection works upon the functional side, and *adapts* them in detail for their places in the local biological economy. There is no obvious reason why selection should not develop small structural variations, though one will not expect specific changes, unless rarely. In general, selection will simply kill out those individuals, whether new species or not, that commence anywhere with functional characters that are unsuited to the conditions of the moment, or that simply have ill-luck. Each new species, by mere heredity, will probably have functional characters more or less closely suited to the place in which it arises, but as time goes on, and the number of species increases, chiefly by arrivals from elsewhere, more and more careful adjustment will be needed to fit in each newcomer. It is in this work that natural selection is of the first importance, doing work that nothing else could do with the same efficiency.

Whether evolution *must* go on in all circumstances, we do not know, for there is evidence like that of the widespread *Hippuris* that seems to show that it is not perhaps absolutely necessary. The evidence of the Podostemaceae seems to show that it *may* go on without change of conditions, though perhaps only under the action of a permanent force. If a plant suddenly arise with a suitability to any particular mode of life, like a climber or a parasite, natural selection will not kill it out, and it may go on living, and perhaps do very well.

As things show more and more definite adaptation to some peculiarity of the conditions, they come up sooner and sooner in their distribution against actual barriers to further spread, so that they tend to occupy lesser areas than older and less adapted species, perhaps closely related to them. As we have seen, a species may become adapted to many regions, one by one (p. 145) as it travels through them, but it need not show this adaptation in external characters, nor have we any reason to suppose that when it has become suited to B it remains necessarily suited to A. It is possible that this functional adaptation, with or without isolation, may result in genic changes that may be added up until they cause a structural mutation. Admittedly we have not yet solved the whole problem of adaptation as one may see it in so many characters, but there is no evidence for the gradual adaptation in structural characters that is demanded by natural selection.

Longley (26) thinks that it will be found that adaptation comes automatically.

Though natural selection comes more and more into play as the species in a given region become more numerous, or as a human society becomes more complex, its action is always primarily individual. There is little or no competition between entire species, varieties, or races (cf. pp. 107, 142, 144).

The conclusion to be drawn, therefore, is that natural selection has not been the driving force under whose influence evolution has been carried on, though it has been the selecting force by whose action the individuals best suited to the conditions of any time and place have been continually picked out. In this way a continual adaptation has gone on, and except in casual and impermanent cases, has ensured that the plants that occur under natural conditions are very closely indeed adapted to those conditions. This adaptation is not structural, but functional, as is illustrated, to take one example only, by the structural resemblance of the members of a large family growing in a great variety of conditions, and the great structural differences of a large ecological "association" of plants growing in very uniform conditions (p. 53). The work of Hutchinson and other agricultural geneticists shows that natural selection picks out a *mixture* of the most suitable individuals, not a type, as indeed may be seen every day in ordinary life by any observant person, and as is shown by the composition of any of the larger nations at the present time.

There are a great many difficulties which to a logical mind are fatal to the supposition that natural selection was responsible for the great evolution of living forms that has gone on. Take for example the facts of economic botany, always dismissed as unimportant since they do not agree with the theory of natural selection. The definite similarities and relationships that exist among the various products belonging to the same family show that whatever was responsible for the production of the family must also be responsible for the economic products, while at the same time the discontinuity in structure of the latter, and the impossibility of gradual transitions between them, shows that their evolution must have been by large mutations. The difference between the distribution of a family and that of an association as given in the last paragraph is another very strong argument in the same direction.

In the second place, natural selection would make the whole great process of evolution, including man, the result of chance

selection of favourable variations, whereas the recent progress of the physical sciences goes to show that in their case the whole evolution is proceeding upon a well-marked "mathematical" programme. The theory that is beginning to be indicated in the work that has been described above, goes to show that evolution also, one of the greatest recent facts of the physical universe, has proceeded upon a course underlying which there is some physical law, probably electrical, which also can be expressed in mathematical terms. This has already been shown to be the case with the law of age and area, which is evidently only a corollary of the larger law thus indicated.

To go on to some of the minor objections to natural selection, of which there are a great number, it is impossible to explain by its aid the characters that divide species, and the difficulty becomes greater and greater as we go up the scale through genus to family and beyond, while at the same time the distinctions become also greater and greater, and any functional value to be attached to them becomes less and less, whilst possible transitions become rarer and rarer.

It is almost impossible to explain the perfection in which the characters show themselves, a clean-cut perfection which again becomes more and more marked the higher we go (p. 76). If natural selection cannot perfect either of such divergent characters as opposite leaves and alternate (showing a definite phyllotaxy), their perfection must be due to heredity, or to direct mutation, for there cannot be a gradual passage from one to the other. In the latter case natural selection is excluded, while in the former one has to remember that the way in which the ancestor obtained the perfect character must be explained by natural selection. There is the further difficulty that so often the two characters occur side by side in species of the same genus. As a special case we may take the family Rubiaceae (p. 118). Members of the family can be found showing alternate leaves (as against opposite, the "family" character), pinnate (entire), intrapetiolar stipules (interpetiolar), male and female flowers (♀), zygomorphic flowers (regular), solitary axillary flowers (cymes or heads), 8-merous flowers (5-4), convolute calyx (open), descending aestivation of corolla (convolute or valvate), anthers by pores (slits), ovary 10-locular (2), endosperm none (present), ruminate (not), whilst the whole family shows an amazing variety in the fruit. All the characters that distinguish the family are found at times to be replaced by something quite different,

whilst at the same time no transitions are possible, a fact which would indicate that all the characters were due to direct mutation. How, then, was the family Rubiaceae, whose actual general characters are those shown in the brackets, evolved by aid of natural selection? If all these vagaries are to be explained on the supposition that morphological necessities override selection, there is nothing at all of structural nature left for selection to act upon. The selectionist is content, and seems to think that his case, that evolution is due to natural selection, is proved, if he can explain a single, and probably very minor character, upon that supposition. He forgets that it also has to explain the correlated characters of a whole family or other systematic group, to say nothing of the great differences that characterise the great divisions of the vegetable kingdom like ferns, mosses, and liverworts, as well as the flowering plants. One cannot employ one machinery to explain one feature or one portion of the vegetable kingdom, another for another.

There is no evidence to show that natural selection is collective in its action rather than individual. It is obviously the latter in daily life, and the work quoted on p. 166 shows that it is probably the same among plants. It seems, therefore, that once the idea that adaptation—ultimately reducible to the chance appearance of favourable variations—is mainly responsible for the distribution of plants and animals has given way to a more scientific conception, the study of plant distribution and of its dynamics will become associated to that of human populations, each giving valuable aid and assistance to the other.

Plants seem to behave like a mixed and more or less casual population expanding in a country where there are barriers of many kinds to interfere with the regularity, and where the distribution is determined in detail by natural selection, working upon the individuals. The same kind of thing has marked the distribution of races in Europe, etc. We have seen that it seems to pick out a mixture, not a type, and we may add to this the curious fact that has lately been exciting some interest, that one kind of cotton may do best when mixed with another (79). This fact may have important bearings upon racial intermingling. One thing at least seems fairly certain, that a whole group A will not conquer and destroy a whole group B, but that the result will be an intermingling of the individuals of both that are best suited to the conditions at the time and place.

Nothing but sudden mutation, usually large, will explain why

the *same* character, and that in perfection, should so often be found at widely separated places in the same family, and not only so, but also at numerous places in other families and in other classes. There is no morphological difference in a berry, whether it be found in the Dicotyledons or in the Monocotyledons.

Only the conception, which is so largely borne out by the facts, that mutations on the whole were larger the further back into the past that one goes, from species through genus to family and class, can easily explain the remarkable fact that this is definitely the case, as both differences, and impossibility of transitions, increase together. Neither in life nor in the fossils do we find any evidence of serious transitional stages, and it is therefore evident that the further back we go from the individual the greater are the differences, whereas natural selection cannot be shown to be more and more efficient in destroying transitions upon the same route.

We have now to consider the actual differences seen between organisms. There is no doubt that specific differences are usually, but *not necessarily*, small (p. 79), while generic are on the whole larger, though there are large differences between different kinds of genera, as for example between those of small families and those of large (p. 110). Family differences are on the whole the largest of the three. Looking at the list of family characters in Appendix I, one notices their divergence when taken in pairs—alternate or opposite leaves, cymose or racemose inflorescence, and so on. Many of these pairs *do not allow* of intermediates or transitions, but this shows less in generic or specific characters. Practically all of the family characters, however, may at times appear as generic or specific; there is nothing about a character to place it only in one of these classes. In fact, as we have seen on p. 110, the rank of genera or of species differs with the size of the groups to which they belong.

One may almost say that a family has a combination of most of these “family” characters, though sometimes the one, sometimes the other, of any particular divergent pair. The important points are this divergence, and the fact that the character is shown in full perfection (p. 114), a feature that one would certainly not expect under the operation of natural selection, for the adaptational value of the character would diminish as it approached perfection, and probably 95 per cent or less would be as good as 100 per cent. It is all but inconceivable that selection should produce perfection in a character, especially one like most

structural characters, in which one can neither find nor imagine any adaptational value whatever.

If differentiation be accepted, the process of evolution may be quickened up considerably, for a single mutation may effect in one step a change which might take an immense time under the action of natural selection, especially when one fully realises that the vast bulk of structural differences have no adaptational value. And if, as upon this view would seem highly probable, mutations were, on the whole, larger as one went further back into past times, the difficulties of explaining the origin of great groups like the ferns will be greatly lessened. It must not be forgotten that these also *must* be explained by natural selection, which as yet has shown itself quite incompetent in this respect. So long as we try to explain these by adaptational changes, or by dying out of transitional stages, so long shall we be in great difficulty. The theory of divergent mutation requires nothing of this kind, and its capacity of explanation is far greater than is that of the theory of gradual adaptation. It seems to the writer that the theory of natural selection leads to too many untenable positions to be any longer acceptable, and that differentiation, working downwards towards the species, and by large mutations, diminishing as one comes downwards (on the whole) should take its place.

The evidence is clearly in favour of differentiation, or divergent mutation, rather than natural selection. The largest and most divergent mutation gives rise on the whole to the family, while the later and usually less divergent ones give rise to the later genera and species, which come as a rule within the limits marked out by the first. This agrees completely with the familiar fact that the key to a family can be so easily made upon these lines, with the largest differences coming first, followed by smaller and smaller ones down to the specific and varietal differences at the bottom. But this feature is a matter of extraordinary difficulty to explain upon the Darwinian theory, under which two species form by progress in gradual adaptation in slightly different directions, the unmodified and the transitional forms being killed out, until at last the difference is so great that they have become new species. But if a slight variation in a favourable direction is enough to give an advantage over the forms that have not varied, what is to be gained by going on with the variation until it becomes specific, and how is this to be done? What adaptational need made one species adopt an alternate leaf with a phyllotaxy of 5/8, its nearest relative opposite leaves?

Nothing but sudden mutation can account for such differences, and natural selection has probably nothing to do with it. It sorts the *products* of evolution into their most suitable places. It is as if the evolutionary train dropped a passenger or two at every station, who has then to make good in the particular conditions that there obtain, in the society or community in which he happens to find himself, and with the equipment for the task that he happens to carry with him.

But if differentiation or divergent mutation be the more correct explanation, it is clear that evolution moved in a direction the opposite of that in which it would move under natural selection. The latter works upward *from* the small variety, which is assumed to be an incipient species, whilst the former works downward *to* the variety. The latter, under differentiation, represents the last ripple of the disturbance which gave rise to the family, not the first ripple which is to give rise to a disturbance becoming ever greater and greater. Natural selection kills out the ancestor and the transitional forms, differentiation does not kill the ancestor, nor expect transitions.

The question as to which explanation is nearer to the truth, therefore, may be settled by an answer to the question as to which was the direction in which evolution moved. To obtain this answer, the author has devised some thirty-four test cases, given in Chaps. x-xiii, and as all of them give good, and a number give very strong, if not convincing, evidence in favour of the direction required by divergent mutation, it becomes in a high degree probable that this is the more correct explanation, and that natural selection had little or nothing to do with the fact that evolution *went on*.

There is some other law behind the latter, which at present we do not understand, though probably when we learn what is the driving force in cell-division, we shall be nearer to the goal. My friend Dr Charles Balfour Stewart suggests that the law is probably electrical, and that perhaps the development of a new form may have some relation to the transfer of energy in some way. The divergence of mutation may perhaps become a little less unintelligible by some explanation of this kind.

To commence with the Numerical test cases (chap. x), it is shown in case i (p. 90) that selection would have great difficulty, as its very name suggests, in causing the evolution of vast and increasing numbers of plants, whilst under differentiation this is automatic, and follows the rule of the hollow curve. In case ii

(p. 94) it is shown that while natural selection can make no predictions, under differentiation it is clear that on the average the size of the largest genus in the family must go with the size of the family itself, which proves to be the case, whilst in case III (p. 95) the gap in size between first and second genera, second and third, and so on, is predicted as, and proves to be, a rapidly diminishing one. In case IV (p. 97) it is predicted, and proved, that the proportions of very small genera, considered as relics under natural selection, must on the average be larger the larger the family, while it would be expected to be the reverse under selection. In case V (p. 99) it is shown that the hollow curve is entirely in favour of differentiation, and in case VI (p. 100) that "Size and Space", a corollary of Age and Area, is equally so. Case VII (p. 100) refers to a paper by Yule and Willis (76), showing that "the manner in which evolution has unfolded itself has been relatively little affected by the various vital and other factors, these only causing deviations this way and that from the dominant plan", a conclusion which obviously does not harmonise with the action of natural selection. Case VIII (p. 101) shows that while on the average the parent genus in small families has as many species as all the rest, more and more genera are required to halve the family when it grows larger. This could be predicted, and is against natural selection. The numerical tests are all clearly in favour of differentiation.

Morphological tests are described in chap. XI. In the important case IX (p. 110), differences in generic rank are dealt with. Natural selection can make no predictions, and simply regards all genera as generic stages in evolution, and of rank as nearly the same as the systematist can compass. Differentiation, however, says that the rank of a genus of a very small family will be approximately equal, on the principle of divergent mutation, to that of the sub-family of a large family. This proves to be the case, giving very strong evidence indeed for evolution by divergent mutation, and showing that the rank of a genus varies with its position, and the size of it and of its family. In case X (p. 114) the fact, hitherto almost totally ignored, is considered, that the characters of plants are generally shown in their perfect condition, and especially so those of the higher groups. This could not happen under selection, to which 95 per cent or less of perfection would be as good as 100 per cent. This is a simple, but destructive argument against gradual acquisition of characters. In case XI (p. 115), the difficulty as to how natural selection got a grip upon

the early stages of non-adaptive characters is considered, and it is pointed out that by differentiation there need not be such stages, nor is adaptation called in. In case xii (p. 118) is considered the case of alternate and opposite leaves, a very common case of divergent characters with no transitions, and where it is almost impossible to suggest any adaptational value in the *difference* between them. Selectionists have to admit that anatomical needs are more potent than adaptational. This question of the relative value of characters has been somewhat ignored. In case xiii (p. 120) staminal characters are dealt with in the same way, and give similar evidence. In case xiv (p. 122), the berry is dealt with, and incidentally it is shown that there is little evidence of adaptation in this phenomenon, so often quoted as an illustration of it. Case xv (p. 124) deals primarily with achenes and follicles. Natural selection could not produce these in their perfect form, nor could it produce the perfect pod, and distinguish between this and the follicle in the marked way that one always finds. In cases xvi, xvii and xviii various other structural puzzles are considered, all much more easily explained by differentiation. In case xix (p. 129) the puzzle of correlated characters in so many of what are usually called adaptations is discussed, and it is shown that while it is quite inexplicable by natural selection, it is somewhat more easy with differentiation, which does not demand an adaptational value in everything. These (adaptation) correlations are useful, while most are not, but some day, perhaps, cytology will bring us the explanation of correlation phenomena.

In chap. xii some further tests are considered under the head of Taxonomy, though largely a continuation of the last. The position of the largest genera of a family is dealt with in case xx (p. 134). On the theory of natural selection one can make no prediction about them, but on that of divergent mutation it is clear that in general they will be widely separated, inasmuch as they will have inherited their characters from the earliest mutations that took place in the family. This is just what proves in general to be the case, as is illustrated by the cases of the Ranunculaceae and the sub-family Silenoideae, etc. In some cases, e.g. *Clematis*, the second largest genus in its family, the genus does not seem to have given rise to a sub-family inheriting its most obvious divergent character, the opposite leaves, but more usually this is the case, and one finds the large genera heading sub-families or other divisions. This is as predicted, whilst natural

selection is quite helpless to explain it. Good evidence is thus given for differentiation. In case xxi (p. 186) the three largest families are shown to occur one in each of the three great divisions of the flowering plants; this seems to indicate the probability of very large mutations in very early divergences. In case xxii (p. 187) the mere fact that one can usually construct dichotomous keys goes to prove differentiation. In case xxiii the fact that divergence from the usual family characters is more pronounced the larger the family, goes the same way. In case xxiv (p. 188) the puzzling but frequent case of parallel variation in one, or in two or three related, families, very difficult to explain by selection, is simple to differentiation, whilst in case xxv (p. 140) widespread organisms are shown to be the simpler, though it does not say much for the advance in organisation supposed to be the result of selection. Darwin himself puts it down to their greater age, as does the writer.

In chap. xiii a few tests based on Geographical distribution are given, but the full development of this attack upon the current theory of evolution must be left for the publication of a book which the writer has in preparation. In case xxvi (p. 146) the difficulties brought up by age and area are considered, especially the fact that on the average the distribution within a country goes with the distribution outside. As the conditions must vary, this goes to show that gradual adaptation other than physiological can have had little or nothing to do with the distribution. Natural selection has had to call in two supplementary hypotheses to explain the facts brought up about endemics and their distribution in Ceylon, and these hypotheses are mutually contradictory. The fact that the distribution of family surnames in Canton Vaud (p. 149) also matches that of plants, including endemics, goes to show that natural selection had very little to do with the latter other than purely locally. In case xxvii (p. 149) it is shown how contour maps may be constructed for most genera, especially when they are small, and have in the vast majority of cases only one centre. As no one genus takes any notice of the contours of any other (p. 154), the contours can hardly be determined by any local conditions. Great Britain, with its great variety of conditions, has nothing but margins of contours. In case xxviii (p. 154), already published, it is shown how the relationships of the smaller genera and of the species in a genus, in any given family, often show such great geographical divergence, with its near relatives separated by distances which

may even be enormous, crossing the oceans, or even the equator. Natural selection could not explain this by any destruction of transitions, for the separations are of all sizes and in all directions. The only simple explanation so far proposed is that the local genera or species are due to direct mutations from the *linking* large and widely distributed genera or species that cover the places in which they occur. This of course involves the acceptance of differentiation. In case xxix (p. 156) it is shown how variety in structure shows no necessary relation to variety in conditions, as one would expect under natural selection. In case xxx (p. 158) the difficulty is pointed out, of explaining, under natural selection, a very common type of distribution. Many genera show one or more widely distributed species, usually very polymorphous, accompanied by local endemic species of the same genus in various parts of their range. The only simple explanation is that put forward by Guppy and by the writer that these endemics have been derived from the widely distributed species by one or more mutations. The incomprehensibility of selection is further developed in case xxxi (p. 161). In case xxxii (p. 161) the inconsistency of the contention that characters are less constant the less useful they are, is pointed out, and in case xxxiii (p. 162) the bearings of Hooker's discovery of the constancy of the numerical relation between Mono- and Di-cotyledons are pointed out, with the fact that there is no monocotyledonous mode of life. Case xxxiv treats of overlap of genera.

It is clear that the tests give very strong evidence indeed in favour of the theory of differentiation or divergent mutation, according to which the course of evolution is in the opposite direction to what has hitherto been supposed, and by mutations which tend to diminish as time goes on, but go in the direction family—genus—species. The organism that first represents the family is, of course, at the same time its first genus and species, but these are of different rank from genera and species in a larger family. By further mutations this will then give rise to further genera and species. The first new genus formed will usually be widely divergent from the parent genus of the family, even if the family be quite small, e.g. of two genera only. Later formations will be less and less divergent on the whole, but will show some of the characters of divergence of their first parents. The main lines of divergence are therefore given by the latter, and later genera fill them in, as shown by a good dichotomous key. As time goes on, new genera will necessarily be evolved at a continually increasing rate, and each, given time enough, may

ultimately become the parent, not only of many species, but of a group of generic offspring forming a sub-tribe or larger division. The whole family will at last end in the tail of genera containing one species each, as shown in the hollow curve. The oldest genera will have the most species, and the number will diminish as does the age, till we come to the tail of monospecific genera.

There is thus very strong evidence to the effect that evolution has gone on without any direct reference to natural selection so far as we can at present see. The new form will appear, whether it be desirable, or suitable, or not, and whether it then survive will depend upon the action of natural selection, with reference to the conditions at the moment. The business of natural selection is (1) to kill out everything in any way unsuitable to the conditions that surround it at the time, either at its first appearance upon the scene, or when a change of conditions occurs; and (2) to adjust to its surroundings, if possible, every new form that comes into the place, whether a new species just born, or a species newly arrived from somewhere else. There is thus plenty of occupation left for natural selection, and in a field where its usefulness and value have never been questioned. The early pioneer species will, of course, get the best chance, and as each newcomer arrives, increasingly close and careful adjustment will be needed, adjustment which natural selection will apply without fear or favour.

Lastly, the evidence is equally strong that in the process of evolution, at any rate as a general rule, the new species formed (which might also be a new genus or even new family if the mutation were a little larger) would appear at one step by sudden mutation. Evolution goes on, but we can see no reason at present that will determine that it shall go in any particular direction, especially in one that shows greater adaptation. The mere fact of the survival of the "lower" forms in such numbers, like mosses, ferns, and liverworts, is against the idea of any rapid progress in adaptation, but probably when an "adaptation" appears, such for example as climbing habit, it will be allowed or encouraged to survive, though why it should appear is at present a mystery.

It is an inspiring thought that so great and complex a process as evolution must have been has not been a mere matter of chance, but has behind it what one may look upon as a great thought or principle that has resulted in its moving as an ordered whole, and working itself out upon a definite plan, as other branches of science have already been shown to do. Darwinism made the biological world a matter of chance. Differentiation,

backed by the universal occurrence of the hollow curves, shows that there is a general law, probably electrical, at the back of it. And if evolution goes on without reference to adaptation values, each genus giving rise to another, and both surviving (as a rule), then the hollow curve becomes an integral part of it. Further refinements must be left to the mathematicians, and will doubtless provide interesting results.

Differentiation is not based upon adaptation at all, the latter remaining a primarily physiological phenomenon. The ordinary type of adaptation, that is familiar to agriculturists, is described in the following extract from a paper by Cockerell. "In California certain scale insects, subjected to poisonous fumes by the horticulturists, have, by a process of the survival of the fittest, developed resistant races, not distinguishable by any morphological characters." The writer was very troubled by cockroaches in his (tropical) house, and used a certain much-advertised poison, but though at first the death-rate was very high, presently there appeared a race of cockroaches that was immune, but looked exactly the same as their predecessors. "The chance of introducing from outside an all-round superior strain diminishes as the adaptation of the local strain to its environment increases" (77, p. 283). Many similar extracts from agricultural papers might be quoted.

There is good reason to suppose that in some way the genes and chromosomes are immediately responsible for the evolution that is going on. Their divisions and fusions strongly suggest some electrical process, with which the suggested action of cosmic rays may have something to do. Or again, something of the nature of genic changes may be going on, and occasionally result in the taking up of "more or less stable positions of equilibrium in cell division" as suggested by the writer in 1907. The apparently purposeless way in which distinguishing characters go together is very like the similar behaviour seen in any mutation involving more than one character. There is no evident reason, nor suggestion of reason, why a Monocotyledon should have at the same time one cotyledon, a trimerous flower, a parallel-veined leaf, and a peculiar anatomy. Nor why Cruciferae should have tetradynamous stamens, *Dryas* eight petals, and so on. Nothing but the direct effect of the genic composition, with heredity, will explain why the characters are shown in perfection.

The continual appearance of characters with complex correlation that could not be due to selection, such as the characters of a

family, genus, or other group, or such as climbing stems accompanied by the means of climbing, goes to show that the family characters, or the climbing habit, must have been produced by some sudden chromosomal change, but by what, and how, determined, we are as yet completely ignorant. Many other "adaptations" come into the same category.

A very probable large mutation, giving the ancestor of what is now a large genus, is that which perhaps gave rise to the columbine (*Aquilegia*), which can easily be imagined as arising from the larkspur (*Delphinium*) by a mutation like that which often gives a symmetrical sport in the toad-flax flower.

It would seem probable that the early future development of the study of evolution will be largely based upon the study of cytology, for it would seem that the conception of gradual adaptation, at any rate in its present form, must be abandoned. The larger groups seem to have appeared before the smaller, upon the whole, the force or size (if one may use such a term) of the mutations that went on diminishing as time went on, the number of smaller mutations on the whole increasing in proportion to the larger. What actual part the external conditions took in the matter is at present inexplicable, but there is nothing in the structural characters, as a general rule, to show that the part was a large one.

One must not lose sight of the hybridisation that is so easily possible, and of which Lotsy (27) made so important a feature in evolution. At the same time, if mutation can take place, as seems highly probable, in such a way as to cross the "sterility line" between species, and so to isolate them, it does not seem very likely that fertile species-hybrids will be produced in such numbers as to have an important influence upon evolution generally, though one must not forget the possible influence of the cosmic rays or other factors in causing the doubling of the chromosome numbers. Hybridisation seems very unlikely among the widely separated genera that seem to be the firstcomers, in most, if not in all, families, but as one goes down the scale, one seems to come among genera that are closer and closer together in their taxonomic characters, and with these hybridisation would seem to become more and more possible, and more likely to occur. Still more would this be the case among the species, and here again rather in the species of large genera. It seems to the writer that this question of hybridisation, with its increasing possibilities in the genera and species of later formation, may be one of some importance, though one must, of course, not forget

that these later genera and species will be of much less wide distribution than the earlier.

The conceptions thus put forward have several possibly even unexpected bearings. If new species and genera can thus arise in widely separated places, though related, there seems no reason why the same character, produced of course by some particular arrangement of genes or chromosomes, should not at times arise from ancestors in which it did not itself occur, i.e. should arise polyphyletically, or from different ancestors. One may even imagine more than one character arising in this way, so as to form, though probably only with great rarity, a polyphyletic genus. In some such way as this one may imagine the case of one genus coming *through* another, as suggested by Bower in the ferns (2). One must remember, too, that what look like species of the same genus and closely allied, need not necessarily be such, and one must compare their chromosome numbers. It is even possible that originally separate types may converge until they may be able to become cross-fertilised.

The sudden appearance of similar mutations at widely separated places may be easily accounted for by a similar construction in the chromosomes of their ancestors, which might give rise to similar mutations. There is no definite reason that one can see—though, of course, this is unfamiliar ground to the writer—why the same genic distribution should not appear in two new species formed from one genus, thus giving rise to a new genus of two species, and possibly even discontinuous in distribution.

Finally, a very strong argument in favour of differentiation, just as with Age and Area, is that by its aid one may make a great many predictions as to what will be found to occur, and find that these predictions are borne out by the facts. A number of such are to be found in many of the test cases given in chaps. x–xiii, and others may be found elsewhere. Now upon the theory of natural selection it is as a rule impossible to make any predictions at all, and when, as for example in several test cases, one may venture a prediction, this is found to be opposed to that made upon the theory of differentiation, and is not borne out by the facts, which always favour the latter theory. This seems to the writer to be a very strong argument in favour of differentiation or divergent mutation. At first, owing to the fact that one has to think, so to speak, in the reverse direction from that to which one has been accustomed (i.e. from family to variety, not from variety to family), it is not always easy, but one soon gets into the new direction of thought.

CHAPTER XV

FINAL SUMMARY OF CONCLUSIONS

1. The world has undoubtedly been peopled by an evolution of forms one from another, giving rise, as time has passed, to beings of increasing complexity.
2. The process of evolution appears not to be a matter of natural selection of chance variations of adaptational value. Rather it is working upon some definite law that we do not yet comprehend. The law probably began its operations with the commencement of life, and it is carrying this on according to some definite plan.
3. Evolution and natural selection are probably to a great extent independent, and they work at right angles to one another, with (in plants at any rate) little mutual interference.
4. Evolution most probably goes on by definite single mutations, which cause structural alterations, which may, but by no means necessarily must, have some functional advantage attached. If such an advantage appear in the mutation, natural selection will likely allow it to survive. There is no necessary reason why the immediate ancestor should die out.
5. Evolution goes on in what one may call the downward direction from family to variety, not in the upward, required by the theory of natural selection.
6. Evolution thus moved in the opposite direction to that required by natural selection, and thirty-four test cases are given, all giving evidence to that effect.
7. Evolution is no longer a matter of chance, but of law. It has no need of any support from natural selection.
8. It thus comes into line with other sciences which have a mathematical basis.
9. The theory of natural selection has been trying to work it backwards.
10. Mutation tends to be divergent, especially in the early stages of a family. The family, consisting probably of one genus and one species, is probably first created by a single mutation, whilst later ones are usually less marked than the first, and give rise to further genera and species. The earliest mutations ultimately give rise to the chief divisions of the family.
11. The Linnean species is not necessarily a conglomeration of forms made from below upwards, but is rather a stage on the way downwards to the Jordanian species.

12. Varieties are the last stages in the mutation, and are not, as a rule, incipient species.

13. Chromosome alterations are probably largely responsible for the mutations that go on.

14. The theory of natural selection is no longer getting us anywhere, except in politics (influence of the dead hand).

15. It comes in principally as an agent to fit into their places in the local economy of the place where they are trying to grow, the forms there furnished to it, whether newly evolved, or only newly arrived, killing out those in any way unsuitable.

16. It has, therefore, not been responsible for the progress that has been made by the actual evolution of new forms, but it has been all-important in fitting them into their places in the economy, which is always increasing in complexity.

17. The theory of natural selection makes evolution a continuous and gradual process, differentiation a discontinuous one.

18. Natural selection (the struggle for existence) works rather upon individuals than on groups. It causes the survival of the fittest population, rather than the fittest type in the mixture.

19. It can make few or no predictions, while differentiation, like age and area, can make many, which are usually successful.

20. Adaptation has been mainly internal or functional, rather than external or structural.

21. Differences in structure do not necessarily mean differences in adaptation.

22. The mutations supposed in differentiation would at one step cross the "sterility line" between species, which has always been a great stumbling block to natural selection; and thus at once isolate the new form, preventing its loss by crossing.

23. Differentiation makes it possible for evolution to go on more rapidly than under natural selection.

24. It explains the great discontinuity seen in the facts of economic botany.

25. It explains the difficulty, almost insuperable to the theory of natural selection, of the increasing divergences of characters as one goes up the scale from species to family.

26. It gets over the difficulty of early stages, and of the frequent correlation of characters, and the need of calling in "morphological necessity"; it does not need to call in adaptation, as the theory of natural selection has to do; and it explains why the large genera are the most variable.

27. It explains the fact that adaptation is so often generic.

28. With its probably genetical basis, it explains the difficulty of the perfect form in which characters, and especially those of the higher divisions, are exhibited, which was almost impossible to the theory of natural selection.

29. It gets over the difficulty caused by the fact that few transition stages are found, either in living or in fossil plants.

30. It explains the universal hollow curve, as well as age and area and size and space, all impossible to the theory of natural selection.

And one may add:

The 34 test cases given often bring out new and sometimes unexpected relations, *e.g.* the grouping of a family (or sub-families if large) into large, medium, and small genera.

Adaptation, isolation, and other phenomena are discussed from somewhat new points of view.

Upon pp. 76, 189, and elsewhere, indications have been given, more or less unintentionally, about things that will only appear in a forthcoming book upon geographical distribution. Therein the writer hopes to show that the adoption of age and area and of differential or divergent mutation, for both of which good proof has now been given, reduces the problems of distribution to a simpler form. By abandoning the supposition, necessarily inherent in natural selection, that plants may be divided into successes and failures, the one expanding and the other contracting the area occupied, all may be regarded as behaving in much the same way as their near relatives. One thus obtains a more satisfactory picture of how evolution and geographical distribution went on, and how they fitted into one another.

APPENDIX I

THE COMMON CHARACTERS THAT DISTINGUISH FAMILIES

The list is made up from the key at the end of my *Dictionary*, and includes the necessary characters to distinguish one family from another. They are arranged as far as possible in divergent pairs, and it will at once be noticed that most of them do not lend themselves to possessing intermediates or transitions.

Herbs, shrubs, trees; parasites, saprophytes, epiphytes, thalloid.
Roots from tap-root, or adventitious.

Stem, rhizome, bulb, etc.; creeping, climbing, or not; herbaceous or woody; jointed or not; mono- or sympodial; angled or not; with latex or resin, or not.

Leaves radical or cauline; alternate, opposite, or whorled; in two ranks, or in three or more; sheathing or not; ligulate or not.

Leaves simple or compound; palmate or pinnate, etc.; entire or lobed or toothed; fleshy or hairy or not; pitchers or not; with oil cavities, glandular dots, with chalk glands, or not.

Leaves stipulate or exstipulate; parallel- or net-veined; dorsiventral or isobilateral; asymmetrical or not.

Inflorescence racemose, cymose, or mixed; ♀ or unisexual; a raceme, corymb, catkin, mono- or dichasial cyme, etc. etc.; with bracts or not; with spathe or not; with bracteoles or not.

Receptacle convex, flat, or hollow; with or without effigurations.

Involucre or none; epicalyx or none; disc or not.

Flower spiral or cyclic; ♀ or ♂ ♀; mon- or dioecious; with perianth or not; homo- or hetero-chlamydeous; iso- or heteromerous; with parts in twos, threes, fours, etc.

Flower regular or zygomorphic; zygomorphism vertical, transverse, or oblique; with rayflorets or not; heterostyled or not; resupinate or not.

Perianth petaloid or sepaloïd, or none.

Calyx whorled or spiral; convolute, imbricate, or valvate; poly- or gamosepalous; odd sepal anterior or posterior.

Corolla of free or united petals; regular or two-lipped; convolute, valvate or imbricate; alternate with sepals, or superposed; corona present or not.

Androphore, gynophore, column, etc., or not.

Stamens in one, two, or more whorls, or spiral; staminodes or not; epipetalous or not; on disc or not; changed to nectaries, etc., or not.

Stamens in one, two, or more whorls; in one whorl all present, or not; spiral and ∞ or not; free, or united in tube or in bundles; diplostemonous or obdiplostemonous; antepetalous (if one whorl) or not; epipetalous or not; on the disc or not.

Stamens branched or not; tetra- or di-dynamous, or not; odd stamen anterior or posterior; staminodes or not; changed to nectaries or not; exploding or not; bent inward in bud, or not.

Anthers dorsi- or basi-fixed, or versatile; extrorse or introrse; mono- or di-thecous; opening by splits, valves, pores, teeth, etc.; connective with or without appendages.

Pollen spherical, polyhedral, etc.; smooth, prickly, warty, etc.; in tetrads, pollinia, etc.

Ovary superior or inferior, etc.; 1-2-3-4-5-more carpels; 1-2-3-4-5-more loculi.

Carpels spiral or in whorls; apo- or syn-carpous; united only by style; 1-2-3-more; transverse or anteroposterior to flower; some abortive, or not; in superposed whorls or not.

Placenta parietal, axile, basal, apical, free-central, etc.; bilobed.

Ovules 1-2-few-many per loculus; in one, two, or more rows as seen in transverse section; stalked or sessile; erect, horizontal, or pendulous; orthotropous, anatropous, campylotropous; on surface.

Raphe ventral or dorsal; micropyle up or down.

Style basal or terminal; present or not, one, or as many or twice as many as carpels; entire or divided; with pollen-cup.

Stigma capitate, lobed, divided, etc.; petaloid or not; sessile or not.

Fruit fleshy or dry; achene, follicle, siliqua, schizocarp, capsule (loculi-septi-cidal, septifragal, etc.), drupe, berry, etc., etc.; dehiscent or indehiscent, etc.; simple or compound; winged or not; with pappus, or hooks, etc.

APPENDIX I

Replum or not; individual carpels divided by horizontal or longitudinal walls, or not.

Seeds per flower, or per carpel 1-2-few-many; albuminous or exalbuminous; with endo- or perisperm; with aril or not, winged or not; hairy or not.

Embryo with one cotyledon or with two; large or small in proportion to endosperm; straight, curved, twisted, folded, etc.

Endosperm oily, starchy, fleshy, cartilaginous, etc.; ruminate or not.

APPENDIX II

CHARACTERS OF FIRST DIVISION INTO SUB-FAMILIES OR TRIBES

Vegetative organs

Land plants—waterplants	Pedaliaceae
Roots—none	Lemnaceae
Green plants—parasites	Convolvulaceae
Climbing—not	Lardizabalaceae, Polemoniaceae
Shrubby—annual	Capparidaceae
Shrubby—undershrub or herb	Juncaceae
Leaves cauline—radical	Flagellariaceae
Leaves 2-ranked—not	Iridaceae, Zingiberaceae
Leaves opposite—usually alternate	Gentianaceae, Myrtaceae
Leaves opposite, stipulate—alternate, exstipulate	Rhizophoraceae
Leaves palmate—simple or pinnate	Bombacaceae, Daticaceae, Lar- dizabalaceae
Leaf-thorns in axil—not	Salvadoraceae
Cystoliths—none	Hernandiaceae
Glandular or stinging hairs—none	Loganiaceae, Urticaceae
Hairs simple or none—usually branched	Cruciferae

Corolla

Free or slightly united—long tube	Dichapetalaceae, Tamaricaceae
Broadly campanulate—salver-shaped	Nolanaceae
Valvate or other aestivation	Ebenaceae, Elaeocarpaceae, Gen- tianaceae
Spurred or not	Papaveraceae, Violaceae
Labellum—none	Styliadiaceae
Petals with appendages—without	Sapotaceae
Petals outside disc—on margin	Burseraceae
Honey-leaves—none	Berberidaceae
Lateral teeth of corolla overlap— underlap	Scrophulariaceae

Fruit and Seed

Berry or drupe—dry fruit	Bromeliaceae, Commelinaceae, Fla- gellariaceae, Myrtaceae, Oxali- daceae, Pittosporaceae, Rhizo- phoraceae, Ulmaceae, Zygophyl- laceae
Other varieties of, or variations in, fruit	Connaraceae, Epacridaceae, Fag- aceae, Geraniaceae, Labiateae, Malpighiaceae, Oleaceae, Pole- moniaceae, Proteaceae, Ranun- culaceae, Valerianaceae, Vochy- siaceae

APPENDIX II

Embryo straight—curved, or otherwise differently shaped	Basellaceae, Butomaceae, Chenopodiaceae, Convolvulaceae, Euphorbiaceae, Droseraceae, Hernandiaceae, Melastomaceae, Solanaceae, Ulmaceae
Endosperm—none	Goodeniaceae, Myrsinaceae, Nymphaeaceae, Ochnaceae, Rhizophoraceae
Endosperm ruminate—not	Polygonaceae
Seeds basal—not	Connaraceae
Seeds embedded in placenta—not	Sonneratiaceae
Seeds in one plane—in more than one	Nolanaceae
Capsule many-seeded—one-seeded in-dehiscent	Caryophyllaceae

These will serve as examples of the degree of divergence of the characters that separate the sub-families or tribes of the various families, without going into too great detail.

APPENDIX III
CHARACTERS OF GENERA IN
BI-GENERIC FAMILIES

Wing on fruit unilateral P 5, bracteoles	Aceraceae Achatocarpaceae	Wing all round the fruit P 4, exc. term. flower. No bracteoles
G (2), style slender, 2- armed	Balanopsidaceae	G (3), style thick, 3-armed, arms bifid
Capsule elastic. Ovules pendulous one above another	Balsaminaceae	Berry. Ovules pendulous side by side
Embryo spiral with nar- row cots.	Cannabinaceae	Embryo curved with broad cots.
K and C alternate. A free	Caricaceae	K and C superposed. A united
Leaves opposite. Plumule thick and straight	Caryocaraceae	Leaves alternate. Plumule long and spiral
Sepals with distinct midrib	Elatinaceae	Sepals with no midrib
Leaves opposite	Erythroxylaceae	Leaves alternate
K in tube. Disc normal	Hippocastanaceae	K free. Disc excentric
P of ♂ 5–8. Ovule basal. ♀ flowers in groups of 4	Julianiaceae	P of ♂ usually 4. Ovule lateral. ♀ flowers in groups of 3
Sta. in one whorl. Ovules free	Hydnoraceae	Two whorls. Ovules sunk in placenta
5-merous	Limnanthaceae	3-merous
Ovary 1-locular	Nyssaceae	Ovary 6–10-locular
C valvate. A 15–80	Quiinaceae	C convolute. A ∞
Disc of few teeth. Sta. few. Bracts entire	Salicaceae	Disc hollow. Sta. ∞ . Bracts divided
Pets. 6–7. Sta. unequally long, anthers by longi- tudinal slits	Scytopetalaceae	Pets. 3. Sta. equally long, anthers by apical slits
Bracteoles. (C). Pollen spiny. Perennial	Stackhousiaceae	No bracteoles. C. Pollen smooth. Annual
Berry	Taccaceae	Capsule
L. opp. C 5, very unequal, one spurred. A to 10	Trigoniaceae	L. alt. C 3, alike. A 3–5
Partial fruit not winged	Tropaeolaceae	Partial fruit with 3 broad wings
Stamens not more than 6 C. 8 stds. G 1-loc. with basal or parietal placenta	Velloziaceae Xyridaceae	Stamens more than 6 (C). No stds. G 3-loc. with axile placenta

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